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NEW OR NOTEWORTHY FUNGI FROM PANAMA AND COLOMBIA. IV

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(WITH 40 FIGURES)

Cystobasidium sebaceum Martin & Couch, sp. nov.

Resupinatum, effusum, pallidum, sebaceo-gelatinosum, siccum inconspicuum; substantio duplici: (1) hyphis conidiophoris anodosis; conidiis subovatis vel irregularis, truncatis, 5–8 × 4–5 μ; (2) hyphis basidiophoris nodoso-septatis; probasidiis subglobosis vel clavatis, parietibus leviter crassis; epibasidiis elongatis, rectis, dein valde inclinatis, demum transverse-septatis; basidiosporis ellipticis, 6–8.5 × 3–4 μ.

Resupinate, thin, waxy-gelatinous, pallid and opalescent when fresh, drying to a thin, almost imperceptible film with white mycelioid margins, about 5 × 2 cm. in extent, with interruptions; in section 40–100 μ thick; texture dense, with basal hyphae parallel with the substratum giving rise to hyphae apparently of two kinds: (1) conidial-bearing, without clamp connections, and (2) probasidial hyphae, with clamp connections; conidia thick-walled, subovate to irregular, with truncate base, 5–8 × 4–5 μ, these forming a continuous layer or aggregated in pocket-like cavities; probasidia formed near surface, with slightly thickened wall, spherical, ovoid, pyriform or clavate, 8.4–16 × 5.8–10 μ, each with basal clamp connection; epibasidia arising at apices of probasidia, usually curved, rarely cylindrical, thicker at distal end and 4-celled by transverse septa, 21–28 × 4–7 μ, not including the slender stalks, variable in length or occasionally lacking, by which they are attached to the hypobasidia, frequently bent abruptly at the junction of the stalk and the main body of the epibasidium, upon which the basidiospores are produced unilaterally, each upon a sterigma 4–6

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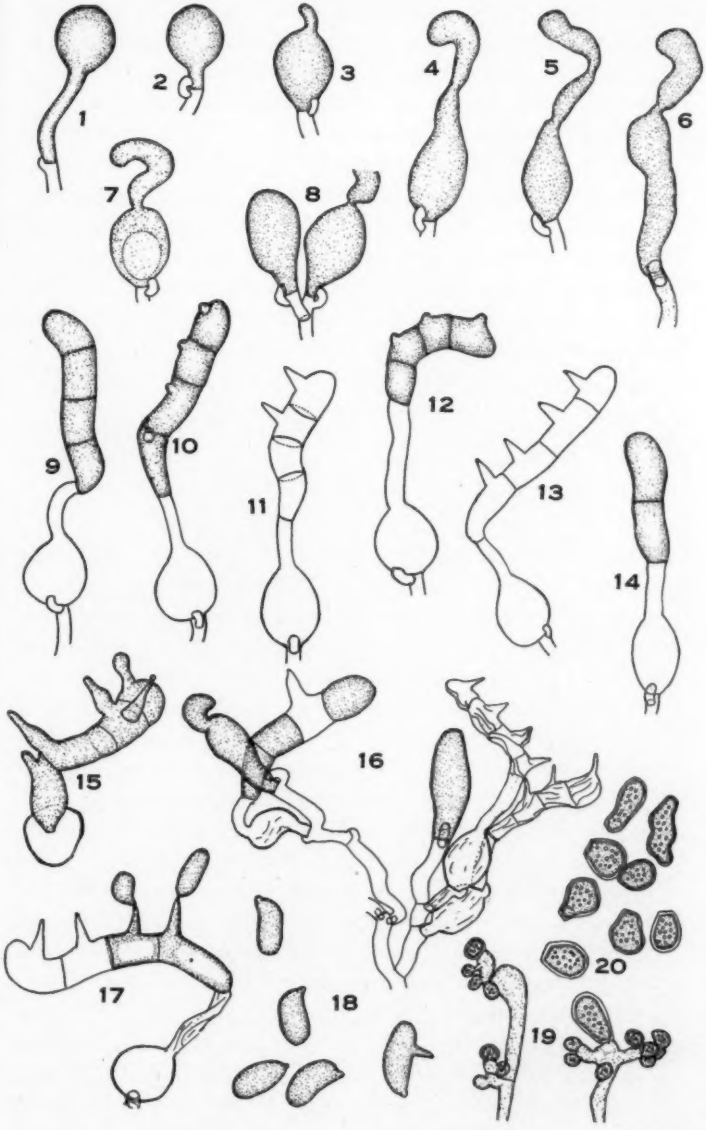
(–10)μ in length; basidiospores hyaline, elliptic, depressed ventrally, with distinct hilum, 6–8.5 $\times$ 3–4 μ.

Colombia: Dept. Magdalena, Hacienda Cincinnati, alt. 1250–1500 m., Aug. 24, 1935. On decaying wood overgrowing remnants of an old *Sebacina*. G. W. M. *3686*, type, in herb. State Univ. Iowa and Univ. No. Car.

Lagerheim (Bih. Sv. Vet.-Akad. Handl. **24**[4]: 15. 1898) established the subgenus *Cystobasidium* to accommodate his new species *Jola lasioboli*, a fungus occurring as a parasite on *Lasiobolus equinus* (Müll.) Karst. in Norway. The essential differences between Lagerheim's species and other species of *Jola* reported up to that time, aside from the fact that the latter are all tropical parasites upon mosses, are the non-gelatinous character of *Cystobasidium* and the nature of the basidia, which in *Jola* arise from thin-walled probasidia and are approximately straight or evenly curved, while in *Cystobasidium* the probasidia are distinctly thick-walled and the epibasidia tend to bend at a right angle at or near the junction of the slender connecting stalk and the fertile, 4-celled terminal portion. Gäumann (Vergl. Morph. Pilze 414. 1926) recognizes *Cystobasidium* as a genus, grouping it with *Jola* and *Saccoblastia* (*i.e. Helicogloea*) in the family Cystobasidiaceae. Dodge, in his revision of Gäumann's work (Comp. Morph. Fungi 546. 1928), maintains the genus, but includes it, with the other two genera named, in the Septobasidiaceae. Couch (Genus Septobasidium 65. 1938) believes that the symbiotic relation of *Septobasidium* with scale insects justifies the separation of that genus from the Auriculariales. The close relationship of *Cystobasidium* with *Jola* and *Helicogloea* may be granted, but the validity of their segregation as a family may be questioned.

When fresh, the collection here discussed was in the form of a thin, grayish white, opalescent, gelatinous sheath, growing on decaying wood and macroscopically indistinguishable from several of the thin, resupinate, waxy-gelatinous forms at present included in *Sebacina*. Under the microscope, however, it proved to possess transversely septate epibasidia arising from thick-walled, vesicular probasidia and connected with the latter by a slender filament as described and illustrated (FIGS. 1–17). The basidiospores apparently germinate by repetition (FIG. 18). The conidia (FIGS. 19–



FIGS. 1–20. *Cystobasidium sebaceum.*

20) have every appearance of being borne on the same fructification, although this cannot be regarded as completely certain. The description of *Jola orthosacca* Rick (Egatea **18**: 210. 1933) suggests a similar fungus, but a collection of the latter kindly sent to me by Father Rick proves to be wholly distinct.

Associated with the transversely septate basidia and the conidia were a few typical cruciate-septate basidia of the tremellaceous type and a mass of disorganized gelatinous material suggesting that the *Cystobasidium* was growing upon an old *Sebacina,* although there is no evidence of parasitism.

I am indebted to Dr. John N. Couch for help in interpreting this difficult form; the drawings illustrating it are his.

PATOUILLARDINA CINEREA Bres.

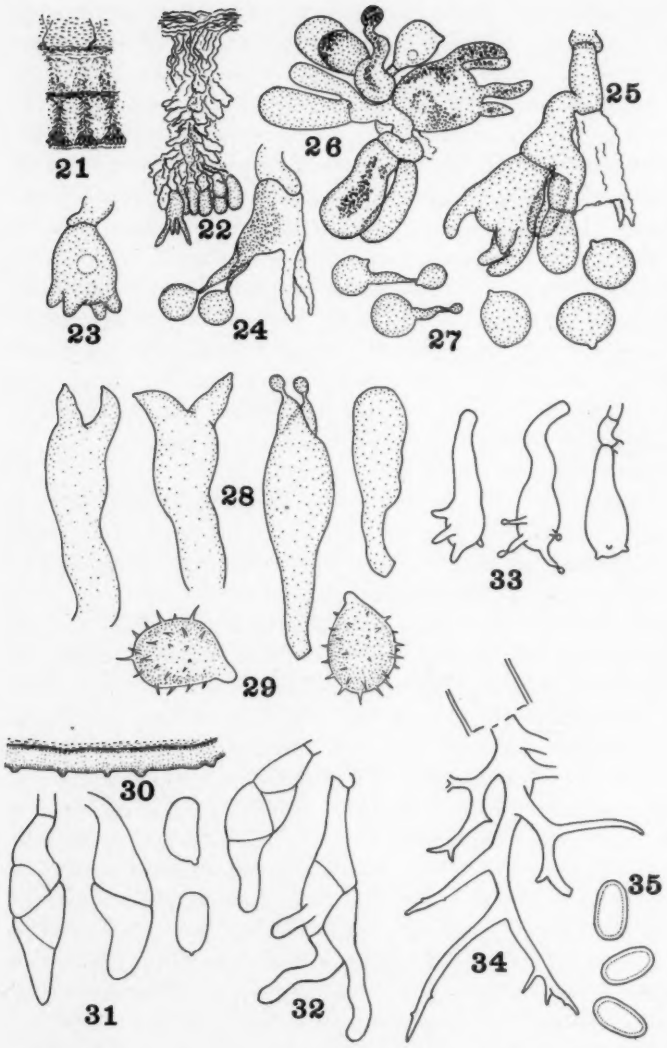
Under the heading "Atractobasidium," Rogers (Mycologia **28**: 398. 1936) has discussed the synonymy of this species. A collection from the island of Taboga (G. W. M. *4480*) affords opportunity for further comment.

The original publication of Bresadola's name was in a paper by Rick (Broteria **5**: 7. 1906). Neither genus nor species is designated as new and no formal descriptions are furnished, but merely informal comment, the essential part of which is as follows: "Dieser . . . Pilz unterscheidet sich makroskopisch nicht von *Corticium* oder resupinatem *Stereum*. . . . Allein die horizontal getheilten Basidien lassen über seine Zugehörigkeit zu den Auriculares kein Zweifel. Es ist ganz eine *Platygloea,* die nicht gelatinös ist." This would scarcely constitute valid publication even if the particulars given were correct. Whether the fact that they are very nearly completely incorrect has any bearing on the validity of the publication, the rules being what they are, may be doubted. In any event, fourteen years later, Bresadola (Ann. Myc. **18**: 52. 1920) wrote formal descriptions of both genus and species, citing the earlier account as the place of original publication, and repeating the errors. Trotter (Sacc. Syll. Fung. **23**: 568. 1925) recognizes the 1920 publication as the valid one, as does Killermann (Engler & Prantl. II. **6**: 108. 1928). In 1917, however, Arnaud (Compt. Rend. Acad. Sci. Paris **164**: 890) had proposed *Patouillardina* as a genus of the Meliolaceae, based on *Meliola clavispora*

Pat. Arnaud's genus is listed, but the reference incorrectly cited, in the Sylloge **24**: 505. On the basis of Trotter's treatment, therefore, Bresadola's name is a homonym. Later, Rick based *Platygloea Grandinia* (Egatea **18**: 211. 1933) and *Protograndinia cinerea* (l. c. 213) on specimens apparently representing the same species but differing in external appearance and particularly in the configuration of the hymenium, the basidia being in all these species described as transversely septate in auriculariaceous fashion.

The genus *Atractobasidium* (Bull. Torrey Club **62**: 339. 1935) was established for a fungus from Mexico with spindle-shaped, obliquely septate basidia in which the secondary septa are consistently at right angles to the primary septum, obviously related to the Tremellaceae rather than the Auriculariaceae. It was only by examining specimens that Baker discovered that the basidia of *Platgygloea Grandinia* were the same, and Rogers (l. c.) established the identity of the other species.

In view of this confusion it is of interest to be able to report on a specimen seen in good condition in the field. The fungus was growing on dead branches of a scrubby tree along the trail to the summit of Taboga just below the point where the scrub gives way to grass. It was definitely gelatinous and the hymenium was covered with small teeth. These, with its general suggestion of a Heterobasidiomycete, led me to label it "*Heterochaete*," under which name it was filed for later study. Under the microscope, the characteristic basidia (FIG. 31) permitted immediate recognition of the genus. Whether there is more than one species involved is still uncertain. When soaked and sectioned, the Taboga specimen is shown to have rather blunt and not at all specialized spines (FIG. 30). A specimen of *Platygloea Grandinia*, collected by Rick in Brazil and now in the collection of the Missouri Botanical Garden, has similar spines, although in scantier number. The hymenium of the type of *Atractobasidium* is practically smooth. The basidia and spores of all three are essentially alike, the differences in size being well within the limits of variation as found in species of this group. It seems permissable, therefore, to consider that these forms all represent a single species, widely distributed in the American tropics, rather variable in external characters, but reasonably uniform in the more fundamental microscopic features.



FIGS. 21–27, *Ceratobasidium plumbeum*; 28–29, *Lachnocladium giganteum*; 30–32, *Patouillardina cinerea*; 33–35, *Nidularia reticulata*.

It must be admitted that it will require a generous extension of the provisions of Art. 43 of the rules to recognize the 1906 publication of *Patouillardina* as valid but it is to be hoped that this may be conceded. It is eminently appropriate that Patouillard's name should be associated with a striking genus of the group which his studies did so much to illuminate. On the other hand, if *Patouillardina* Bres. is to be rejected in favor of Arnaud's use of the name, then the genus must be known by Rick's name *Protograndinia,* thus perpetuating the discredited theories of Brefeld, whose meretricious treatment of the group has been largely responsible for the tardy recognition of Patouillard's work.

Ceratobasidium plumbeum sp. nov.

Fructificatione resupinata, viva plumbea, sicca atra; probasidiis clavatis, 12–15 × 9–11 μ; epibasidiis crassis, cornutis vel subfusiformis; basidiosporis globosis vel late ellipsoidis, 6–8 μ diam., per repetitionem germinantibus.

Broadly but interruptedly effused, indeterminate, deep grayish-olive when soaked, drying dull olivaceous black or fuscous black, in section about 75 μ thick, or, when stratified by the superposition of a second layer over an older one, 150 μ thick; structure consisting of a thin layer of basal hyphae parallel with the substratum, 10–15 μ thick, an intermediate layer composed of erect, pillar-like strands bearing collapsed basidia and separated by a gelatinous matrix and supporting a continuous hymenial layer; probasidia broadly cylindrical or clavate, borne in terminal clusters, with conspicuous, proliferating clamp connections, finally 12–15 × 9–11 μ, developing four, rarely three or two, thick, conical or subfusiform epibasidia, usually tipped with a sterigma and basidiospore, but some remaining sterile; basidiospores with a conspicuous apiculus, globose, 6–8 μ in diameter, or broadly ovate or depressed, up to 9 × 8 μ, germinating by repetition.

Panama: Canal Zone, in low forest 3 k. east of Arraiján, Sept. 1, 1937. G. W. M. *4597,* type. In herb. State Univ. Ia. and Missouri Bot. Gard. Growing on under side of decaying log.

The genus *Ceratobasidium* was established by Rogers (Univ. Iowa Stud. Nat. Hist. **17**: 4. 1935) to include certain resupinate Basidiomycetes having unseptate basidia bearing stout, cornute or spindle-shaped epibasidia and with basidiospores germinating by repetition. As Rogers points out, the genus is intermediate between the Heterobasidiomycetes and the Homobasidiomycetes, but

although its affinities are rather with the former group than with the latter, under the system of classification commonly used at present, it must be included in the Thelephoraceae, itself a tentative and badly limited family that must eventually be discarded.

The present species is strikingly characterized in section by the hyphal pillars, perpendicular to the substratum, bearing clusters of basidia at the apex (FIGS. 21, 22), proliferating from the conspicuous clamp connections (FIGS. 25, 26) and surrounded by the collapsed basidia throughout their length, much as is the case in certain species of *Bourdotia*. Although four epibasidia are commonly formed, there is a suggestion that all do not function, while later spores, apparently mature (FIG. 24), are apt to be small. This, as well as the reduction in size due to germination by repetition, may account for the great variation in spore size, a common phenomenon in the Heterobasidiomycetes and much less common, although not rare, in the Homobasidiomycetes.

Many of the hyphae and the older, emptied basidia, and occasionally some probasidia are more or less densely charged with a blackish-brown granular deposit (FIG. 26), causing them to look yellowish-brown under the lens and doubtless largely responsible for the dark appearance of the fructification as a whole.

EPITHELE DUSSII Pat.

According to Burt (Ann. Missouri Bot. Gard. **6**: 265. 1919) known only from Gaudeloupe and Venezuela. An ample collection on dead leaves of a royal palm on the grounds of the Missouri Botanical Garden Tropical Station at Balboa (G. W. M. *4215*), while sterile, is certainly an *Epithele* and is almost certainly the present species. The fructification, thickly studded with the striking, sterile, tooth-like fascicles, is broadly effused, as was the Venezuelan specimen studied by Burt.

CRATERELLUS CORNUCOPIOIDES Pers. ex Fries

The range of this common temperate species is given by Burt (Ann. Missouri Bot. Gard. **1**: 334. 1914) as "Canada to South Carolina and Missouri." Three collections from western Panama, on the slopes of El Volcan in Chiriquí, two at about 1700 m. and one at 1900 m., notably extend the known range and emphasize the temperate element in the fungous population of the tropical mountains.

LACHNOCLADIUM GIGANTEUM Pat.

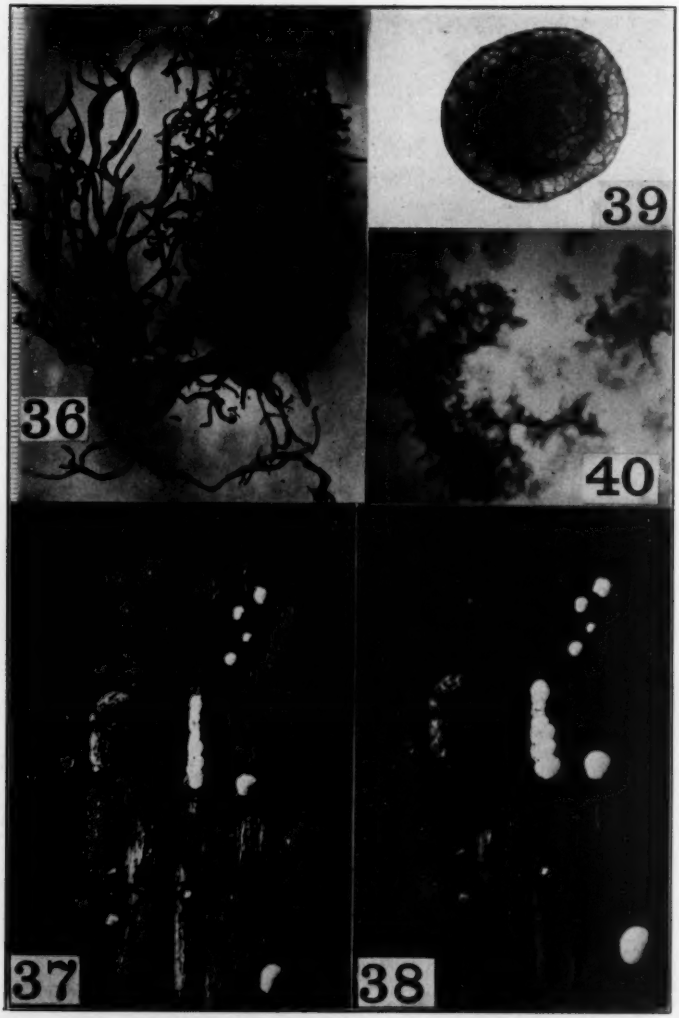
Originally reported from French Guiana (Jour. de Bot. **3**: 34. 1889), this species is not included by Burt among the North American forms. The single collection I refer to it was collected by A. M. Bouché, Jr., in the Valle Chiquita, south of El Valle de Antón, Prov. Coclé, Panama, in July, 1935 (G. W. M. *2989*, FIG. 36). While I have not been able to compare it with authentic material, the large size, the stout stipe from which the dichotomous branches arise, the blackish-brown color when soaked and the large brown spiny spores agree satisfactorily with Patouillard's description and the accompanying illustrations. Patouillard includes the species in his section *Dendrocladium*, characterized in part by a unilateral hymenium. In the specimen under consideration, the hymenium is unilateral below, but amphigenous nearer the tips.

The basidia are very striking. At first cylindric-ovate on a sharply constricted stalk, they become clavate and develop two thick apical branches (FIG. 28), much like the epibasidia of the Dacrymycetaceae, but shorter, at the tips of which are small, but distinct sterigmata, each of which bears a spore. The spores are yellowish-brown, the body, including the thick, blunt apiculus, which is often attached at an abrupt angle, 13–16 × 8–10 μ. The long spines are sparsely and somewhat irregularly disposed (FIG. 29). Patouillard's spore measurements are slightly but not significantly smaller, 12–15 × 8–9 μ.

Burt (Ann. Missouri Bot. Gard. **6**: 267. 1919) believes that species of *Lachnocladium* with dark-colored, rough or muricate spores are better referred to *Thelephora*. Useful as spore characters are, the nature of the basidium is even more fundamental, and the present species would be as foreign to the typical Thelephoras as it is to the Lachnocladiums with smooth hyaline spores. For the present it seems unnecessary to remove it from *Lachnocladium*.

NIDULARIA RETICULATA Petch.

This species has heretofore been known from a single collection from Ceylon. It was originally reported by Berkeley and Broome (Jour. Linn. Soc. **14**: 81. 1873) as *N. Duriaeana* Tul. (Ann. Sci.



FIGS. 36, *Lachnocladium giganteum*; 37–40, *Nidularia reticulata*.

Nat. III. **1**: 99. 1844). Petch submitted a portion of the type collection to Lloyd (Myc. Writ. 2. Letter **19**: 1. 1908), who pronounced it wholly unlike Tulasne's species, whereupon Petch (Ann. Royal Bot. Gard. Peradeniya **7**: 60. 1919) described it as new.

The collection which I refer to this species was growing on the fallen sheath of a banana at Balboa, C. Z., in August, 1937 (G. W. M. *3985*). The basidiocarps, while small, are rather conspicuous when young, because of their pure white color. Later, by the gelatinization of the peridium, they take the pale brownish color of the peridioles, and are then inconspicuous. They are subglobose, finally 2 mm. or slightly more in diameter, or up to 4 mm. by anastomosis. The peridium dries as a very thin, horny, transparent sheath which becomes gelatinous and pallid when soaked (FIGS. 37, 38). The peridioles are lenticular, unattached, 0.45 to 0.55 mm. in diameter and 0.2 mm. thick and bright yellowish-brown when soaked. Under low magnifications they have a striking appearance, well brought out in the accompanying photograph (FIG. 39). The surface appears to be strongly reticulate, with a broad translucent margin surrounding a denser central portion. A section at right angles to the broader dimension shows that there is a thin membranous outer wall from which arise stout, brown, antler-like hyphae, about 10 μ in diameter at the bases, which branch repeatedly, but with little or no anastomosis, forming a floccose intermediate layer (FIGS. 34, 40). The inner layer, about three or four cells in thickness, appears to be wholly free from the intermediate layer, but gives rise directly to the pseudoparenchymous subhymenium, of approximately equal thickness. The hymenium is clearly defined, composed of a single compact palisade layer of basidia. The basidia (FIG. 33) bear four spores in somewhat irregular fashion. The spores (FIG. 35) are hyaline, cylindrical, thick walled, without apiculus, 8.5–9.5 $\times$ 4.5–5.5 μ.

There are minor differences between the Panama specimens and those from Ceylon. Berkeley and Broome give the spore size as .0003 $\times$ .0002 inches (*i.e.*, about 7.5 $\times$ 5 μ). Petch states that the peridioles are up to 0.75 mm. in diameter, noting, however, that the Peradeniya specimens appear to be immature. Lloyd (l. c.) states that an antler-like middle layer is known elsewhere

only in *Nidula emodensis* (Berk.) Lloyd, which is otherwise quite distinct. Tulasne (l. c. *pl. 7, f. 12*) shows similar structures in *Nidularia australis* Tul., from Chile, which, both in Tulasne's drawing (l. c. *pl. 7, f. 2, 3*) and in Lloyd's photograph (Myc. Writ. 2. Nidulariaceae 9, *f. 8*) shows strong resemblance to *Nidula*.

Since in most respects the Panama specimens agree very closely with *N. reticulata* as described by Petch, and since the differences are no greater than might be expected from two widely separated collections, it seems advisable to regard both as representing a single species.

EXPLANATION OF FIGURES

Figs. 1–20. *Cystobasidium sebaceum.* 1–8, various forms of probasidia with early stages in development of epibasidia; note clamp connections at base; 9–13, later stages in development of epibasidia; 14, two-celled epibasidium; 15, epibasidium with two sterigmata arising from penultimate segment; 16, cluster of basidia in various stages; 17, mature basidium with spores partly discharged; 18, five basidiospores, one germinating by repetition; 19, development of thick-walled conidia; 20, detached conidia, showing variation. Drawn by J. N. Couch, × 1000.

Figs. 21–27. *Ceratobasidium plumbeum.* 21, diagrammatic longitudinal section through fructification, showing a second layer overgrowing an old layer, × 110; 22, a single pillar showing basal layer, collapsed basidia and surface hymenium, × 460; 23, young basidium with epibasidia developing; 24, older basidium with two collapsed epibasidia from which basidiospores have been discharged, protoplasm apparently still passing into remaining two basidiospores; 25–26, two clusters of basidia showing proliferation from clamp connections; 27, five basidiospores, two germinating by repetition. Figs. 23–27, × 1000.

Figs. 28–29. *Lachnocladium giganteum.* 28, young basidium, at right, and three older stages; 29, two spores. Both × 1000.

Figs. 30–32. *Patouillardina cinerea.* 30, diagrammatic section through fructification of No. *4480* from Taboga, × 8; 31, two basidia and two spores of same, × 1000; 32, two basidia from a collection of *Platygloea Grandinia* Rick, collected by Rick in Brazil, × 1000.

Figs. 33–35. *Nidularia reticulata.* 33, three basidia; 34, base and tip of antler-like hypha from peridiole wall; 35, three basidiospores. All × 1000.

Fig. 36. *Lachnocladium giganteum,* no. *2989.* Slightly reduced, the scale at left is in millimeters.

Figs. 37–40. *Nidularia reticulata,* no. *3985.* 37, immature fructifications, at right, and mature ones, at left, dry, × 4½; 38, same, soaked, at same magnification; 39, peridiole, mounted whole × 50; 40, antler-shaped hyphae from crushed mount of peridiole, × 50.

THE SQUIRREL AS A NEW HOST TO A RINGWORM FUNGUS

EDWARD D. DELAMATER

(WITH 3 FIGURES)

A. INTRODUCTION

During the year 1936 and 1937 a noticeable number of the common gray squirrels living on and near the Johns Hopkins University Campus at Homewood, Baltimore, were observed to have a serious skin infection. During the spring of 1936 sick animals were obtained, but no causative organisms were retrieved in culture, due to overgrowth of saprophytes. Fungi were, however, observed in the skin on direct examination.

During the following winter, 1936–1937, the disease was observed to be still rampant. On March 19, 1937, a sick animal was again obtained for observation and mycological study begun. It was found that the squirrel represents a new host to the ringworm fungi.

B. THE DISEASE

1. *Macroscopic appearance of lesions in the squirrel:* The lesions observed in squirrels were typical of tinea. They were widespread and definitely circinate. The borders of adjacent lesions ran into one another and produced large irregular confluent patches. The lesions were not localized, as in similar diseases of the horse, for example, but covered practically every part of the body. The dorsal, ventral, and lateral aspects of the body were widely infected, the fore and hind limbs, the tail, the throat, and face. Nearly all the infected squirrels observed had lesions similarly extended (FIG. 1).

The lesions themselves had the following aspects: They were extensively epilated, leaving much of the body surface devoid of fur. The epilated lesion surfaces were covered by a dense coat of small scales. There were no heavy exudative crusts. Under

the scales the infected skin was dotted by multiple pin-point vesicles. The lesion borders, studded with solitary remaining hairs, were slightly raised and slightly inflammatory (FIG. 1).

2. *Microscopic:* Upon direct examination of scales and hair, observed by placing scrapings on a slide in 10–15 per cent NaOH, numerous ramifying filaments of the invading fungus were observed. In the scales these filaments tended to fragment into chains of arthrospores, giving the appearance of a closely packed chain of cuboidal beads; the adjoining cells were in close abutment.

In infected hairs the fungus was seen both within and around the hair shafts. When in the hair the filaments were again fragmented into chains of cuboidal arthrospores, which followed tortuous channels through the hair shaft. When outside, the elements were in the form of a closely packed sheath of small (microide) spores lying just below the hair cuticle. Usually the arthrospores of the spore sheath were so closely packed as to have lost their filamentous relationship. Here and there, however, their filamentous origin was still apparent.

Autopsy: Material was taken of a diseased part; sections were made and stained by the methods of Heidenhain (hematoxylin-eosin) and of Gram. The observations just recorded for direct examination were verified. Figure *2B* is a photo of an infected hair from the autopsy sections. The chains of fungous spores are seen to lie in the hair shaft.

C. THE CAUSATIVE FUNGUS—ISOLATION

The causative fungus as it appears in the lesions has just been described.

In obtaining the fungus in culture two methods were used. In the first, the lesions were carefully swabbed with 80 per cent alcohol and then scraped with a sterile scalpel. The scrapings were placed in the surface of honey agar slants (Sabouraud) and incubated at room temperature. When a suspicious looking growth was observed amongst the concurrently growing saprophytes, it was carefully isolated and inoculated into new tubes, until pure cultures were obtained.

In the second method, lesion scrapings were rubbed directly into the scarified surface of the skin of three guinea pigs. This

Fig. 1. Gray squirrel infected with *T. mentagrophytes* (*gypseum*).

method served also as a test for direct disease transmission and virulence and will be considered presently. The infected animals were carefully observed every day. When it appeared certain macroscopically that a disease had been successfully passed, direct microscopical examination was made as above and cultures were taken. By this method the same fungus was obtained both from the squirrel directly and from the infected guinea pigs. Tests were then made on fresh guinea pigs with the fungus obtained in pure culture from both the original squirrel and the experimental animals. Pure cultures were again retrieved from this series. The pathogenicity of the fungus isolated was proven and Koch's postulates fulfilled.

THE FUNGUS IN CULTURE

2. *Macroscopic:* When cultured on Sabouraud's honey or maltose agars the colonies are characteristic and similar and are typical of *Trichophyton mentagrophytes* (*gypseum*) Robin, Sabouraud. This cultural character along with the previously noted ectothrix microide character of the fungus in the hair, aid in the taxonomic placement of the fungus. The surface of the colony is flat and very powdery. At the periphery the edges are frayed radially. The color is white or cream to buff. Figure 2*A* is a photograph, natural size, of such a colony three weeks old. The back side of the colony characteristically shows a wine-red color.

On corn meal or potato agar the aerial growth is less profuse and the colony color is more nearly white. The red pigment appears in potato agar cultures but not in corn meal agar cultures.

3. *Microscopic morphology:* The microscopic morphology of *T. mentagrophytes* (*gypseum*) is just as characteristic as the colony in Sabouraud's agar and in general offers few obstacles for identification, a confusing synonomy of specific names notwithstanding.

Honey and maltose agar cultures: These media give nearly identical results both culturally and morphologically. All of the structures represented by the drawings in figure 3, with the exception of 3*D* are found on these media. Figure 3*A* is a typical branching cluster of aerial hyphae. Figure 3*B* represents an intermediate stage between this and the characteristic en grappes cluster of aleuriospores (microconidia) represented in figure 3*C* (1, 2, 3).

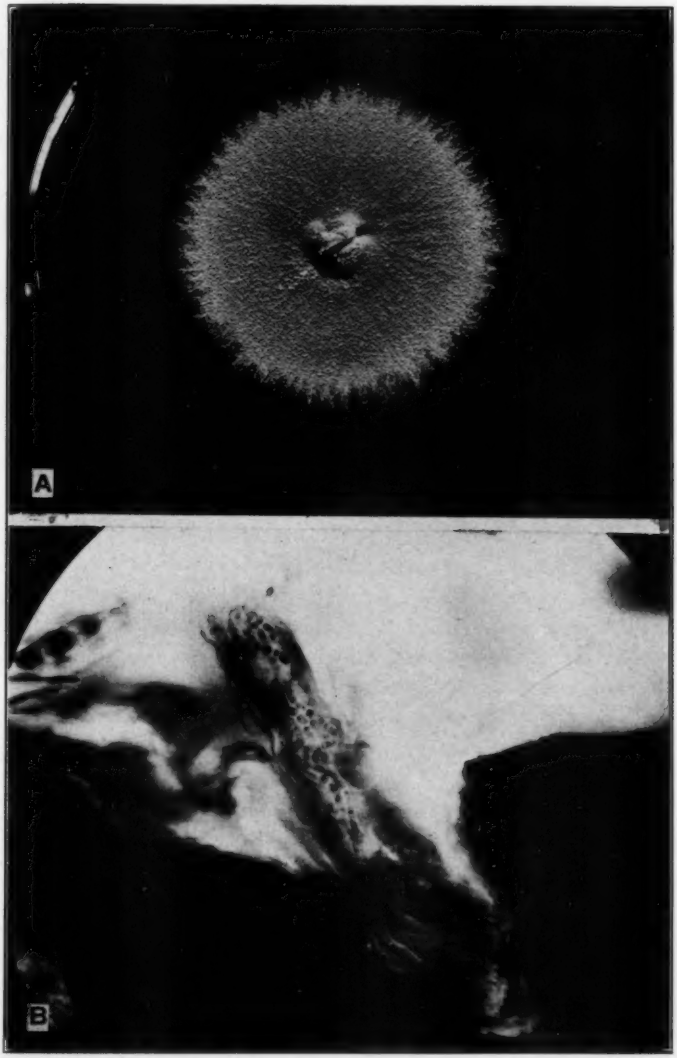


Fig. 2*A*. 20 day old maltose agar culture *T. mentagrophytes* (*gypseum*).
Fig. 2*B*. Biopsy section of squirrel lesion showing infected hair.

The swollen cells bearing aleuriospores shown in 3*D* was not observed on these media. Figure 3*E* represents various configurations of the thyrse or acladium type of aleuriospore fruiting so typical of nearly all the dermatophytes. Figure 3*F* represents the racquette mycelium typical of these fungi, but also found in the Gymnoascaceae and in *Coccidiodes immitis,* etc. Figures 3*G* and 3*J* are two types of chlamydospores, the terminal and intercalary, respectively. Figures 3*H,* 1 and 2, are spirals showing wide dissimilarity in configuration. Figure 3*I* is a so-called nodular organ, so suggestive of an abortive sexual phase. These structures simulate closely the early sexual development as seen in the lower Ascomycetes (Plectascales). Figure 3*K* shows typically irregular subsurface hyphae. These are deeply imbedded in the substrate, are thin-walled and suggest an absorptive function. Figure 3*L* shows the typical fuseaux (macroconidia) of the *T. gypseum* group. The occurrence or relative profuseness of these structures may vary appreciably between different strains of the same fungus. In corn meal agar, in contrast to the wealth of morphological structures just described for honey and maltose agars, several structures are not formed. There are no swollen, aleuriospore bearing hyphae, fuseaux, nodular organs, and relatively few spirals. In potato agar only nodular organs are missing, although spirals are less frequent than on other media. Swollen, bulbous, aleuriospore bearing cells (FIG. 3*D*) are present, but not abundant. This is the only media on which they were observed.

D. VIRULENCE OF THE FUNGUS

DeLamater and Benham [1] have reported numerous experiments on the experimental disease produced by this and related fungi. These need not be detailed here, but certain facts deserve brief consideration.

Direct transmission of the disease from the infected squirrel to guinea pigs by using infected scales has been noted, and also that the disease was reproduced by the direct application of material

[1] DeLamater, E. D. & Benham, R. W. Experimental studies with Dermatophytes. 1. Primary disease course in laboratory animals. 2. Immunity and hypersensitivity produced in laboratory animals. Jour. Inv. Derm. 1: 451–488. 1938.

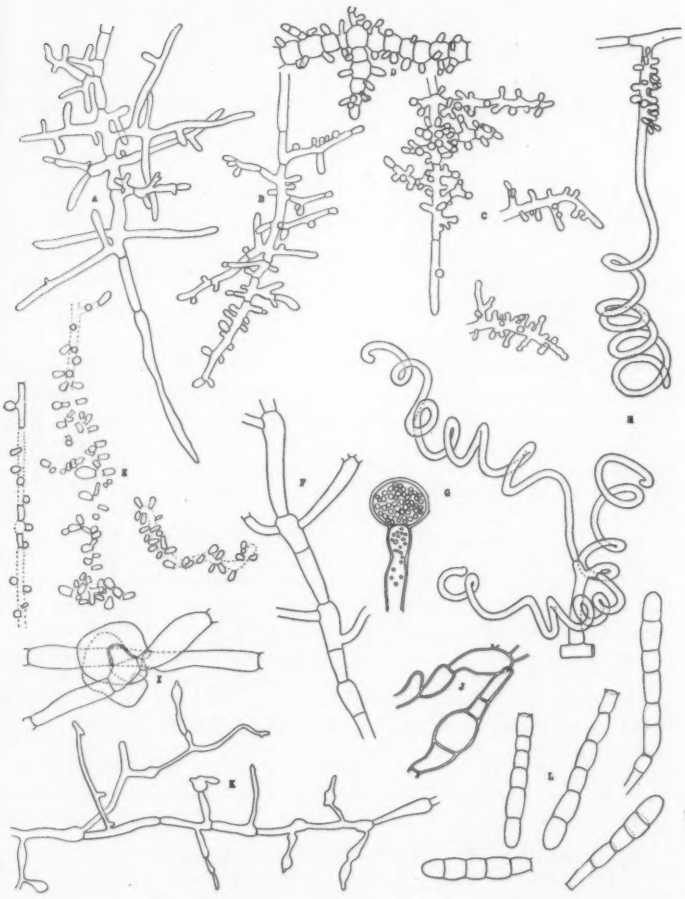


Fig. 3*A–L*. Microscopic structures found in *T. mentagrophytes* (*gypseum*) on various media.

from pure cultures. In addition, it should be stated that normal animals not only in direct contact with infected animals, but also several in separate cages at a distance of two or more feet from the infective source became ill. This gives a rough idea of the virulence of the fungus, even though the spores were wind blown (or otherwise transmitted) and no previous scarification was done

for the purpose of aiding the "take." The character of the disease produced was further evidence of the virulence of this fungus.

Cats and rabbits were also shown to be susceptible to this strain of *T. gypseum* and in two cases accidental infection of human subjects occurred.

SUMMARY [2]

The squirrel is described for the first time as host to an already well known ringworm fungus, *T. mentagrophytes* (*gypseum*) (Robin-Sabouraud).

EXPLANATION OF FIGURES

Fig. 1. Photograph of infected squirrel showing extent and character of lesions—about ½ natural size. Fig. 2*A*. Photograph of a 20 day maltose agar (Sabouraud) culture, natural size, showing characteristic cultural characters; 2*B*. Biopsy section of squirrel lesion showing infected hair (endothrix); about 1200 ×. Fig. 3*A*. Aerial hyphal clump, corn meal agar, one month; about 300 ×; *B*. Transitional stage between Fig. 1 and 3, corn meal agar; about 300 ×; *C*1, 2, 3. En grappes cluster of aleuriospores (microconidia), corn meal agar, one month; about 300 ×; *D*. Swollen cells bearing aleuriospores, 3 week potato agar culture; about 300 ×; *E*. Thyrse—acladium type aleuriospores (microconidia), one month corn meal culture; about 300 ×; *F*. Racquette mycelium (aerial or surface), corn meal agar, one month; about 300 ×; *G*. Terminal chlamydospore containing oil droplets. Honey agar culture, one month; about 600 ×; *H*1. Spiral with basal cluster of microconidia, one month corn meal agar culture; about 300 ×; *H*2. Multiple spirals; *I*. Nodular organ, 4 month honey agar culture, suggesting abortive sexual phase; about 600 ×; *J*. Intercalary chlamydospores (subaerial), granules, one month corn meal culture; about 300 ×; *K*. Subaerial hyphae, 4 month honey agar culture; about 600 ×; *L*. Fuseaux (macroconidia), one month honey agar; about 300 ×.

[2] A complete reference list of the material available on animal infections due to the ringworm fungi will appear soon with a review of the subject, in the Botanical Review.

A NEW SPECIES OF LAGENIDIUM PARASITIC ON ROTIFER EGGS [1, 2]

F. K. SPARROW, JR.

(WITH 15 FIGURES)

While the majority of the Lagenidiales are parasitic on species of fresh water algae, a few have been observed on microscopic animals, as for example, *Myzocytium vermicolum* Zopf, on eel worms, and *M. zoopthorum* Sparrow, on eggs and adults of the Rotiferae.

In May, 1937, a virulent parasite belonging to this order developed in rotifer eggs occurring in gross cultures of aquatic debris collected in the Huron River near Ann Arbor, Michigan.

The infecting agent is a relatively large, laterally biciliate zoöspore of the "secondary," "grape-seed-like" type (FIG. 15), practically identical with that formed by species of *Pythium*. Upon coming to rest on the outer wall of the egg the spore encysts and very soon produces a short, blunt germ tube which pierces the wall of the intended host (FIG. 1). The broad tip of this tube then increases in width and, as the contents of the extramatrical cyst are gradually conveyed into it, assumes a spherical shape (FIGS. 2, 3). The transference of this material into the egg takes about fifteen minutes. Inside, the walled sphere of fungous protoplasm rests in contact with the living, maturing rotifer. Within two hours the parasite has doubled in size and definite signs of body disorganization of the animal and cessation of rhythmic pulsation are apparent. As the thallus enlarges, the contents of the egg are absorbed (FIGS. 4–7) and eventually only a few brownish granules remain. During development of the thallus, particularly in cases where only a single infection has occurred and hence where ample space is available, broad lobes are formed on the somewhat ellipsoidal or irregular body. The contents of the fungus which during early stages of

[1] Paper from the Botany Department, University of Michigan No. 686.

[2] Acknowledgment is made to the Faculty Research Fund for financial aid given in connection with the preparation of this paper.

development were somewhat transparent and watery in appearance become as growth continues dark, dense and full of irregular, refractive granules.

At maturity, the thallus consists of a single celled, sac-like body with one or more broad lobes (FIGS. 8, 9). When several thalli occupy a single egg, a not uncommon condition, little or no tendency towards lobulation is noted (FIG. 8). If conditions are favorable, the whole structure is soon transformed into a single sporangium. During maturation a broad discharge papilla is formed which pierces the wall of the egg. At its apex, which just protrudes from the egg, a crescent-shaped layer of refractive material appears, beneath which is a clear area. In the later stages of development isolated vacuoles appear and disappear and the protoplasm eventually becomes finely granular and shot throughout with minute refractive granules (FIG. 9). A few minutes before spore discharge furrows are visible which delimit what are probably the spore initials. This is quickly followed by the sudden appearance of a large central vacuole which extends throughout the whole structure, the protoplasmic contents at this stage appearing in optical section as crenulations along the inner walls (FIGS. 10–11). After a few seconds the vacuole suddenly disappears and the protoplasm becomes homogeneous save for regularly placed, shadowy areas about the size of the spore initials. At this moment, the hyaline tip of the discharge tube enlarges, loses its double contour and refractivity, and evacuation of the contents is initiated (FIG. 12). The protoplasm flows out smoothly and steadily, forming outside a constantly enlarging spherical mass. Before all the protoplasm has been discharged, the spore initials are visible in the material outside and these almost instantly become separated into somewhat angular bodies (FIG. 13). Around the periphery short, hyaline cilia may be seen actively undulating (FIG. 14). The whole mass of discharged spores, consisting at times of seventy-five to one hundred or more individuals, assumes a rocking motion to which is eventually added a slight rotation. No vesicle has been observed. After ten minutes, or less, the zoöspores, which have now become somewhat separated but are still in a spherical or hemispherical cluster at the orifice of the sporangium, gradually increase their speed of movement and each

quickly assumes a rapid lateral vibratory motion. There then ensues a period of only a few seconds duration of extremely rapid vibration which terminates with the dispersal in all directions of the zoöspores. No sexual reproduction or resting structures were observed.

RELATIONSHIPS

In its type of non-sexual reproduction and superficial aspect within the eggs, this organism resembles *Myzocytium zoopthorum* Sparrow (**3**). This is particularly true when more than one thallus develops in a single egg. In such cases a marked resemblance to figure 8, plate 19 of *M. zoopthorum* is apparent. However, no septation of the thallus was ever found in the numerous examples studied, and it remained one celled throughout. Indeed, where only a single thallus took possession of an egg, and where presumably, because of the large amount of available food and space, unlimited development could take place, only broad lobes were formed. One and two celled thalli of *Myzocytium proliferum* Schenk have been figured by Zopf (**5**) but these are obviously non-typical, abberent forms. Evidences for a multicellular development were searched for in particular in the egg parasite but none was found.

Comparison with the remarkable Copepod parasite *Oovorus copepodorum* Entz (**1**) cannot be made, since from the account given of the fungus, no intramatrical vegetative body is described.

The rotifer egg parasite resembles to a marked degree *Lagenidium Oedogonii* Scherffel (**2**). In this algal parasite, an irregularly ovoid or sac-like or occasionally tubular thallus develops which often forms in fully mature examples broad finger-like lobes. Eventually, the whole structure is converted into a single sporangium the contents of which, after a series of vacuolate stages essentially like those in the present fungus, are discharged through a single (rarely two) evacuation tube. Typically, the zoöspores complete their maturation at the orifice of the discharge tube and in some instances at least, are surrounded by an evanescent vesicle. Scherffel has also observed in what he considers the same species that in rare cases the spores undergo a period of swarming within the sporangium and then emerge individually to form as in *Achlya*,

a group of motionless cysts at the mouth of the discharge tube. Resting spores, produced by a sexual process similar to that of *Olpidiopsis* have also been observed by Scherffel. No well defined fertilization tube, such as is ordinarily formed for example in *L. Rabenhorstii* is developed and in this feature it approaches most species of *Olpidiopsis*.

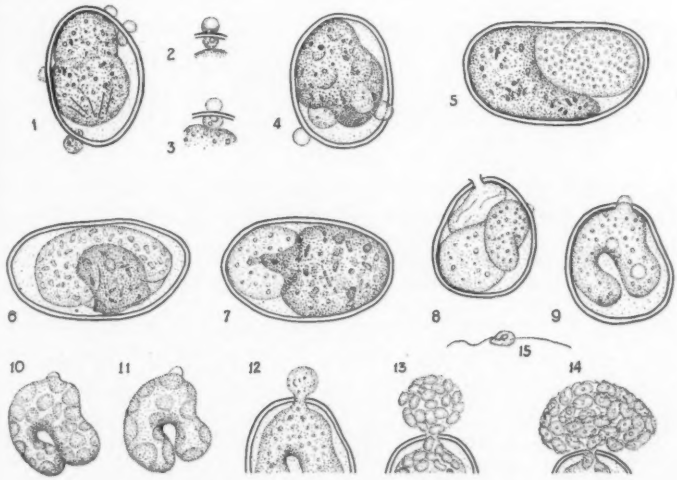
Lagena radicicola Vanterpool and Ledingham (**4**) a parasite of wheat roots, exhibits a one-celled body plan essentially similar to the rotifer egg parasite and *Lagenidium Oedogonii*. Like the last named, it remains attached to the host wall at the point of infection during its development, a ring of host wall material being produced which aids in maintaining this connection. Further, the method of zoöspore formation, the zoöspores, type of sexual reproduction and oöspores differ in no essential features from one-celled species of *Lagenidium*. *Lagena* does differ however from *L. Oedogonii* in that (1) the point of attachment of the parasite is also the place of formation of the discharge tube of the sporangium and (2) in sexual reproduction a definite antheridial tube is produced by the male thallus which makes contact with the receptive structure. It should also be noted that in *Lagena* the two conjugating bodies are of equal size whereas from what little is known of *L. Oedogonii* the male is smaller than the female.

It seems evident therefore, that no great morphological differences separate the one-celled algal inhabiting species of *Lagenidium* from the parasite of wheat roots, *Lagena*, or from the parasite of rotifer eggs. All agree in having a one-celled, sac-like lobed or tubular thallus which becomes converted into a single sporangium. Typically, all discharge their laterally biciliate zoöspores in *Pythium*-like fashion and, where sexual reproduction is known, this is by conjugation of thalli. While an antheridial tube is formed in *Lagena*, in contrast apparently to *L. Oedogonii*, this may be so reduced, if the gametes are in contact, as to be only a slight swelling.

Since recent investigations clearly indicate that there are one-celled species of lagenidiaceous organisms which are typically one-celled, and are not so because of poor environmental conditions as Zopf's earlier work indicated, the advisability of segregating

them from *Lagenidium* arises. *Lagena*, with a few slight changes, would readily accommodate them and in the future such a course may prove highly desirable. Further investigations on the process of sexual reproduction in these one-celled forms are necessary, however, before such a change should be made.

Since the parasite of rotifer eggs appears distinct in the shape and size of its sporangium, size of its zoöspores and perhaps physiologically as well from other one-celled lagenidiaceous fungi, it is considered a new species, *Lagenidium oophilum*, or, if *Lagena* ultimately becomes a repository for these organisms, *Lagena oophila*.



FIGS. 1–15. *Lagenidium oophilum*.

Lagenidium oophilum sp. nov.

[3] Thallus aut singulus, irregulariter saccatus vel ellipsoidalis lobatusque, lobis crassis longitudine variantibus, aut thalli aggregati subregulariter ellipsoidales plerumque non lobati, holocarpice transformati in singula sporangia hyalina 20–40 μ longa, 12–25 μ lata, cum papilla brevi 4–5 μ diam. sessili vel paululum producta praedita; zoosporis forma seminibus Vitis generis similibus, lateraliter biciliatis, 8 μ longis, 6 μ latis, singillatim ejectis sed gragatim ad tubi os maturantibus, ut videtur a vesciculis non circumdatis; cystospora 5–6 μ diam. Reproductionem sexualem non vidi.

[3] I am indebted to Prof. H. H. Bartlett for the preparation of the Latin description.

Parasiticum, in ovis embryonibusque rotiferorum, in flumine "Huron" prope urbem Ann Arbor, Michigan, Maio 1937.

Thallus when occurring singly somewhat irregularly saccate or ellipsoidal, with broad lobes of varying length, when several, more regularly ellipsoidal and often unlobed; converted holocarpically into a single thin walled, colorless sporangium 20–40 μ long by 12–25 μ wide with a short sessile or slightly prolonged discharge papilla 4–5 μ in diameter; zoöspores grape seed-like, laterally biciliate, 8 μ long by 6 μ wide, discharged individually and undergoing a period of maturation in a group at the orifice of the discharge tube, apparently not surrounded by a vesicle; cystospore 5–6 μ in diameter; sexual reproduction not observed.

Parasitic in eggs and embryos of rotifers, Huron River near Ann Arbor, Michigan, May 1937.

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5. **Zopf, W.** Zur Kenntniss der Phycomyceten. I. Zur Morphologie und Biologie der Ancylisteen und Chytridiaceen. Nova Acta Acad. Leop.-Carol 47: 143–236. *pl. 12–21.* 1884.

EXPLANATION OF FIGURES

Fig. 1, Rotifer egg with several encysted zoöspores of *L. oophilum.* Penetration of the egg has been accomplished in two instances; 2, 3, stages in infection of the egg; 4–7, thalli in various stages of development; the darker plasma of the host is gradually being absorbed; 8, egg with a lobed thallus and an empty, unlobed, sporangium; 9, nearly mature thallus; 10, 11, vacuolate stage of sporangium just before discharge; 12, beginning of zoöspore discharge; 13, later stage of discharge; 14, discharge nearly completed, the first emerged zoöspores maturing their cilia; 15, free swimming zoöspore. All figures × 560. Figures inked in by Richard Higgins.

PHOTOGRAPHS AND DESCRIPTIONS OF CUP-FUNGI—XXXIV. A NEW HUMARINA

FRED J. SEAVER

(WITH 1 FIGURE)

During the latter part of November and early December, 1938, the writer had the privilege of making a third visit to Bermuda in continuation of the explorations of the mycoflora of those islands. Among the oustanding species of fungi collected was one belonging to the above named genus. It was unusual in that it seemed to be restricted entirely to the seeds of a cultivated palm, while most of the other species of the genus occur on humus or decaying material of various kinds. Like some other species of the genus it is attractive because of its rather brilliant color. It differs so much from any known species of the genus that the writer is here offering it as new to science. The description is as follows:

Humarina Waterstonii sp. nov.

Apothecia occurring singly or in cespitose clusters, sessile or subsessile, early expanding and becoming shallow cup-shaped or subdiscoid, reaching a diameter of 4–5 mm., externally whitish; hymenium slightly concave, bright red, almost scarlet; asci cylindric or subcylindric, reaching a length of 300 μ and a diameter of 16 μ, tapering below into a stem-like base 8-spored; spores 1-seriate ellipsoid, slightly narrowed toward either end densely filled with oil-drops and granules, smooth, hyaline about 14–16 $\times$ 24–26 μ; paraphyses about 2 μ in diameter gradually enlarged above to 4 μ.

Apotheciis sparsis aut caespitosis, sessilis vel subsessilis cupulatis vel subapplanatis, 4–5 mm. diam.; hymenio leniter concavo, rubro; ascis cylindricis, octosporis 300 $\times$ 16 μ; sporis monostichis, ellipsoideis, multiguttulatis, levibus, 14–18 $\times$24–26 μ; paraphysibus clavatis 2–3 μ diam.

On partially buried seeds of *Livistona chinensis*.

This species is dedicated to Mr. J. M. Waterston, the local pathologist in the Experiment Station at Bermuda, in recognition

of his loyal coöperation and the many courtesies extended to the writer on his recent visit to Bermuda. The species was found to be abundant on the seeds of the Chinese palm, *Livistona chinensis,* in cultivation close to the laboratories of the Experiment Station.

SPORE DISCHARGE

The present species offers a fine illustration of what might be called a "pop-gun" method of spore discharge, described in the North American Cup-fungi, pages 20 and 21. From the accompanying illustrations, all of which were made with the aid of a camera lucida, the great discrepancy between the size of the ascostome, indicated by the diameter of the operculum, as compared with the diameter of the spore which has passed through the ascostome is quite apparent. The operculum is scarcely half the diameter of the spore. This means that in passing through the ascostome it is necessary for the spore to stretch this opening to twice its original diameter. When the spore has passed half way through it will naturally contract and pop the spore out with accelerated force. That this stretching and contracting has taken place is evident from the fact that the ascostome is always intact after the spores have passed through. The force which drives the spore through the ascostome is supplied by the osmotic pressure within the ascus. Sometimes the force seems to be expended before all of the spores have been discharged and, as shown in the upper right hand figure, occasionally a spore is caught in the very act of "nosing" its way through the ascostome. This theory does not imply that there is any considerable pause between the discharge of each individual spore. They must proceed in single file, but are usually discharged in one continuous series, and apparently at one time, except that occasionally as indicated above the force is not sufficient to drive all the spores through the narrow trap-door which nature has provided for their exit.

This species has some characters in common with those of the tropical genera *Cookeina* and *Phillipsia,* especially the relatively small size of the ascostome. The eccentricity of the ascostome, which seems to be a constant character in those forms, is not so

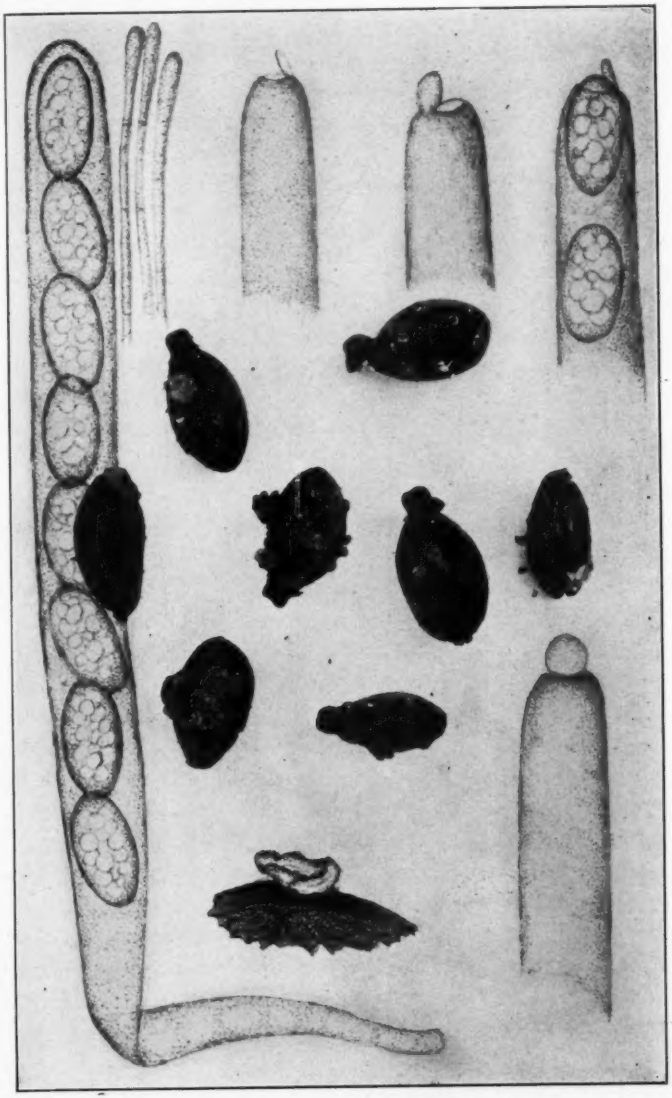


FIG. 1. *Humarina Waterstonii.*

in the Bermuda species, although at times it is more or less eccentric.

THE NEW YORK BOTANICAL GARDEN

EXPLANATION OF FIGURE

Center, photo of several infected seeds slightly enlarged; left, an ascus with spores and paraphyses greatly enlarged; upper right, an ascus which had discharged all of the spores except two, one of which has its nose through the ascostome; below center, sketch of two apothecia enlarged; also three views of empty asci showing the ascostome and operculum from different angles.

TWO NEW FUNGI ON LEGUMES

L. R. Tehon

(with 6 figures)

Continued field examination of crops brings to light from time to time, in obviously parasitic rôles, fungi that appear not to have been observed previously. These newly discovered parasites usually do not have, and may never have, large importance. Yet with other minor pests they contribute measurably to the reduction of yields by disease; and on crops such as legumes, which have value as soil builders, they exert an indirect and intangible influence concerned with more than yield alone. As causes of disease the two fungi described here, one injurious to alfalfa leaves, the other a destroyer of Korean lespedeza plants, affect yield but little; their importance lies, rather, in their effect on the vigor of plants relied on to improve soil.

PLACOSPHAERIA ON ALFALFA

During the growing seasons of 1935, 1936, and 1938 an alfalfa leaf disease was found, the general appearance of which suggests the familiar tarspot of maple (fig. 1). Leaflets become infected at one or more points, most commonly, however, only on one side of the midvein. The invaded portion of the blade turns yellow and then collapses between the veins, and the leaf surface assumes a finely corrugated appearance. Distal to the infection the blade shrivels and tends to crack and fray. Later, small areas within infected regions turn black; and the blackening spreads until, in some instances, it occupies nearly half the side of a leaflet. Blackening takes place simultaneously on both the upper and lower surfaces, and as it progresses an abnormal thickening of that part of the blade occurs. In mature material the blackened surfaces are broken irregularly by roundish or fissured openings large enough to be visible under a 10 × magnifier.

Microtome sections reveal (FIGS. 2, 3) that within and near the blackened areas all of the leaf tissues, except the cuticles and the woody cells of the veins, have been destroyed and have been replaced by a compact stroma. Internally, the stroma is a hyaline plectenchyma; but next to the cuticle on each side (FIG. 3) lie one to several layers of more robust, less closely compacted dark-walled cells. Beyond the blackened area less destruction of the leaf tissues has occurred, and the stroma is less perfectly formed.

Spore-bearing cavities (FIG. 4) develop within the stroma and open through either the upper or the lower leaf surface but not through both. Morphologically, these cavities are simple locules; but two or more, merging during development, may appear as a compound locule. They are not sharply differentiated from the stroma; there is only an abrupt transition from the surrounding plectenchymatic cells to conidiophores. Spores are borne apically on the conidiophores and issue in cirrhi from the locule openings. True ostioles are not formed; but, because of the smallness of the openings and the relative permanence of the stromatic rind, the locules are more logically considered as immersed pycnidia than as acervuli.

In classification, this fungus is to be allied with the genus *Placosphaeria*. In 1904 Sydow [1] described *Placosphaeria Lupini* on *Lupinus sparsiflorus* Benth. from Eldorado County, California; but in 1922 he and Petrak [2] transferred the lupine fungus to *Stictochorella*, in which the stroma is superficial, after examining material on living leaves of *Lupinus ornatus* Dougl. from the state of Washington. Since now no authentic species of *Placosphaeria* is recorded on any legume, it is necessary to name the alfalfa parasite as follows:

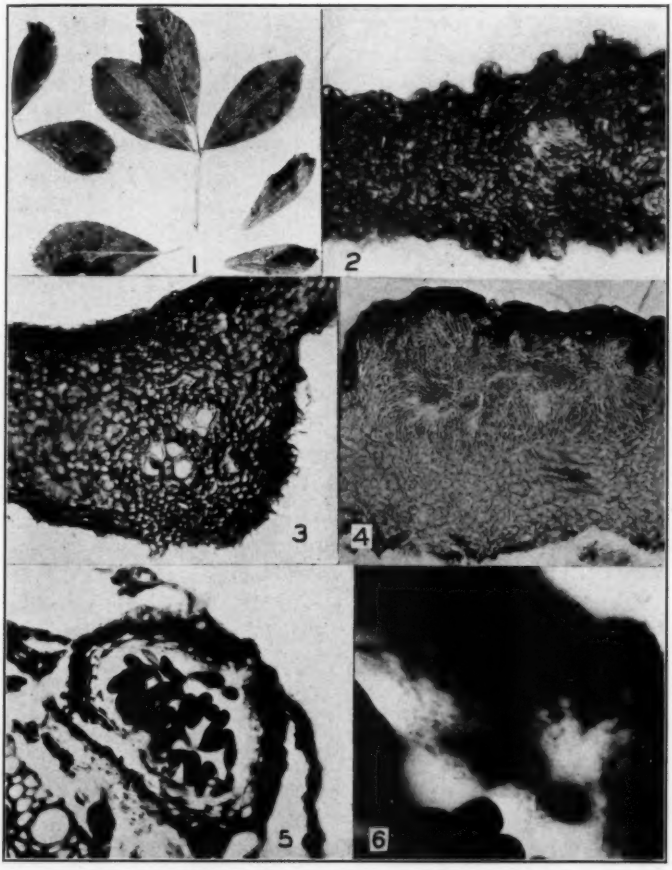
Placosphaeria Medicaginis sp. nov.

Stromatibus in foliis innatis, nigris, variabilibus et irregulariter effusis, rarius confluentibus, tantum 1 cm. longis, multilocularibus; loculis numerosis, amphigenis, sphaericis vel deplanatis, plerumque simplicibus vel saepe confluentibus et apparentibus compositis, 75–140 μ latis, 75 μ altis, spurie ostiolatis; sporulis oblongis, hyalinis, continuis, 3–7 μ longis, 1.5–2 μ latis.

[1] Sydow, H. & P. Novae fungorum species. Ann. Myc. **2**: 162–174. 1904.

[2] Sydow, H. & F. Petrak. Ein Beitrag zur Kenntnis der Pilzflora Nordamerikas, insbesondere der nordwestlichen Staaten. Ann. Myc. **20**: 178–218, 1922.

On *Medicago sativa* L.[3]—Freeburg, St. Clair County, Illinois, October 22, 1935, Accession No. *25,276* (type); Malta, DeKalb



FIGS. 1–4. *Placosphaeria Medicaginis;* 5–6, *Catosphaeropsis caulivora.*

County, Illinois, July 17, 1936, Accession No. *26,977;* Centralia, Marion County, Illinois, April 29, 1938, Accession No. *26,704.*

[3] Collections and field notes were made by G. H. Boewe. Accession numbers designate specimens in the Mycological Collection of the Illinois Natural History Survey.

The three records of occurrence, made, as appears from the above, in different years and in fields separated by as much as 250 miles, indicate a wide distribution for the fungus. In the St. Clair County field 40 among 100 counted plants bore diseased leaves; and on these plants 33 out of 300 leaves, or 11 per cent, were diseased as illustrated. In the DeKalb County field 42 per cent of the counted plants bore the disease; and on these plants 27 among 894 leaves, or about 3 per cent, were infected. And in the Marion County field 94 per cent of the counted plants bore diseased leaves; and 78 among 300 examined leaves, or 26 per cent, were infected.

CATOSPHAEROPSIS ON KOREAN LESPEDEZA

Increased planting of Korean *Lespedeza* for soil improvement during recent years has focused attention on the diseases that attack it, and in 1937 the stem blight here described was discovered.

On stems of still living plants lesions first appear between the nodes as elongated areas slightly darker in color than the normal reddish-brown of the stem. Lateral branches show similar but correspondingly smaller lesions, and are soon killed. Eventually all parts of a plant that lie beyond a stem lesion die. As lesions extend and develop, they become dotted with minute black pycnidia, which often are arranged rather definitely in longitudinal rows. At about the same time, the leaves wither and fall off. The stipules wither and die, also, but remain on the stem; and the presence of the disease in advanced stages is grossly signalized, in the field, by the sight of leafless stems and branches clothed in dry, yellow stipules.

In microtome sections of diseased stems mycelium is seen chiefly in three regions: in the cortical collenchyma and parenchyma, between the epidermis and the sclerenchymatic pericycle; in the phloem, cambium, and newest xylem, between the pericycle and the lignified xylem; and in the hollow center of the stem, from which the pith and primary xylem have disappeared.

In the first of these regions hyphae penetrate between and into the cells, kill them, and bring about such disintegration that, in the vicinity of pycnidia and often elsewhere, hardly a vestige of the original tissues can be seen. In the cambial region hyphae bring

about complete destruction of the phloem and cambium and partially dissolve the outer, less lignified cells of the xylem; and finally complete separation of the outer tissues from the xylem occurs. And in the hollow pith hyphae form a loose layer on the inner face of the xylem, where they destroy the remnants of pith parenchyma and primary xylem.

There is, also, direct connection between these layers of mycelium. Since the pericyclic sclerenchyma is not a continuous band, hyphae penetrate to the cambium by way of the parenchyma that intervenes between bast masses, killing and disorganizing the parenchyma cells among which they pass. And hyphae extend by way especially of the vascular rays, but also by way of other xylem cells, from the cambial region to the pith.

The pycnidium (FIG. 5) develops as an inverse structure, in connection with the mycelial plate between the cuticle and the pericycle. At maturity it is somewhat more than hemispherical, with an incomplete base closely affixed to an underlying sclerenchyma bundle. Its wall is membranous and is composed of three or four layers of cells. The cells of the outer two layers are roundish, heavy-walled, brown, and 10–15 μ in diameter, while those of the inner layers are more elongated, thin-walled except for slightly thickened corners, and less conspicuously brown-tinted. At its apex the pycnidium is at first thickened and raised into a low papilla, as if a true ostiole were being formed; but the papilla eventually breaks or is forced off, leaving an irregularly circular opening for the emission of spores. The sporogenous hyphae (FIG. 6), instead of lying at the base of the pycnidium, line its dome; and the spores cut off from the conidiophores of this layer are brown, oblong, and single-celled.

Although superficially this fungus presents the characters of *Sphaeropsis,* and might be so classified if not fully examined, the incompleteness of its pycnidium and its upside-down method of sporulation place it definitely in the Leptostromataceae; and in this family it seems capable of placement only in the Pycnothyriae of Diedicke.[4] This relationship is supported also by a character of the mycelium. Although the hyphae in the interior of the host are essentially cylindrical, those next to the cuticle frequently form

[4] Diedicke, H. Die Leptostromataceen. Ann. Myc. 11: 172–184. 1913.

plate-like masses intimately connected with the wall of the pycnidium; and in these plates surface filaments present that peculiar structure, termed "radiate" or "aliform," that is recognized as a prominent characteristic of the Hemisphaeriales.

Since it may reasonably be supposed that many of the named species of *Sphaeropsis* also have the characteristics described for this new fungus, it might be thought that the most convenient disposition would be to include it in that genus; but the writer believes that, for accuracy in classification, recognition in the Leptostromataceae of the characters presented by this fungus is desirable.

Catosphaeropsis gen. nov.

Genus Leptostromatacearum cum sporulis brunneis, magnis, et continuis ut in Sphaeropside; pycnidiis membranaceis, hemisphaericis, basim non completis; stratis sporogenibus in fornicibus pycnidiorum sitis; et hyphis extimis radiantibus vel cellas aliformes exhibentibus.

Catosphaeropsis caulivora sp. nov.

Pycnidiis in caulibus, sparsis vel saepius in serie longitudinali ordinatis, conspicue pertusis, 120–200 μ diametris, atronitidis et cuticula solim indutis sed in regione corticis delapsi nutricis evolventibus, plusquam hemisphaericis et basim incurviusculis, in apice primitus papilla clausis sed in maturitate poro irregulariter circulari usque 25 μ diametro evacuantibus; muris membranaceis, non carbonaceis; stratis conidiferis superne in fornice epigentibus; conidiis brunneis, continuis, oblongis usque ovatis vel basim angustis, 16–27 μ longis, 9–12 μ latis; hyphis subcuticularibus hyalinis usque brunneis, abunde septatis, in schedis radiantibus vel aliformibus conniventibus.

On *Lespedeza stipulacea* Maxim.—Crossville, White County, Illinois, July 22, 1937, Accession No. *26,978* (type); Metropolis, Massac County, Illinois, September 9, 1937, Accession No. *26,979*.

The importance of this fungus in the two fields in which it has been observed is indicated by the notes accompanying the two collections. In the field from which the type material was taken, a count of 1000 plants showed that only 0.1 per cent were diseased; but in the other field, examined a month and a half later, 11 per cent of the plants were diseased.

SECTION OF APPLIED BOTANY AND PLANT PATHOLOGY,
THE ILLINOIS NATURAL HISTORY SURVEY,
URBANA, ILLINOIS

EXPLANATION OF FIGURES

Figs. 1–4. *Placosphaeria Medicaginis.* 1, alfalfa leaflets showing various degrees of infection and bearing the black stromata typical of the fungus; 2, section through a young part of a stroma, illustrating the nearly complete dissolution of leaf tissue; 3, section through the mature portion of a stroma, illustrating the destruction of all but the cuticles and woody vein-cells of the leaf, and the development of the stromatic rind; 4, section through a mature stroma, showing two epiphyllous sporiferous locules that merged during development.

Figs. 5–6. *Catosphaeropsis caulivora.* 5, a section, not quite vertical, through a pycnidium, illustrating the incomplete base (torn loose from the sclerenchyma), characteristics of the wall and the spores, and the absence of a basal sporiferous plectenchyma; 6, inner wall, in section, near the top of a pycnidium, illustrating the location of the sporiferous layer in the dome of the pycnidium.

STUDIES IN THE PURPLE-BROWN SPORED AGARICS [1]

ALEXANDER H. SMITH

(WITH 6 FIGURES)

During the past five or six years considerable attention has been given to the fragile purple-brown spored agarics of Michigan, but, due to confusion in the literature both in America and abroad, progress in identifying the collections has been slow. Because of this confusion, I have limited myself largely to interpretations of American species based on studies of the type collections, and have not found it advisable to attempt to make critical comparisons of American with European species. In *Psathyra stipitissima* and *Psathyrella subatrata,* however, such comparisons have been necessary.

I wish to express my thanks to Prof. H. M. Fitzpatrick of Cornell University, Ithaca, New York, for the opportunity to study Atkinson's collections and for the photograph of *Hypholoma confertissimum* Atk.; to Dr. H. D. House of the New York State Museum, Albany, N. Y., who very kindly placed Peck's collections at my disposal, and to Dr. F. J. Seaver of the New York Botanical Gardens, New York City, for access to the types of the species described by Dr. W. A. Murrill. All color names within quotation marks are taken from R. Ridgway, *Color standards and color nomenclature,* Wash., D. C., 1912. The collection numbers are those of the writer unless otherwise stated. The specimens have been deposited in the University of Michigan Herbarium.

PSATHYRA MICROSPERMA Peck, PSATHYRA MULTIPEDATA Peck, PSATHYRA STIPITISSIMA Lange and HYPHOLOMA CONFERTISSIMUM Atk.

Psathyra microsperma and *P. multipedata* have been reported and illustrated for Michigan (**1**) (**7**). My determination (**7**) of the former species was based on a collection made near Ann

[1] Papers from the University of Michigan Herbarium.

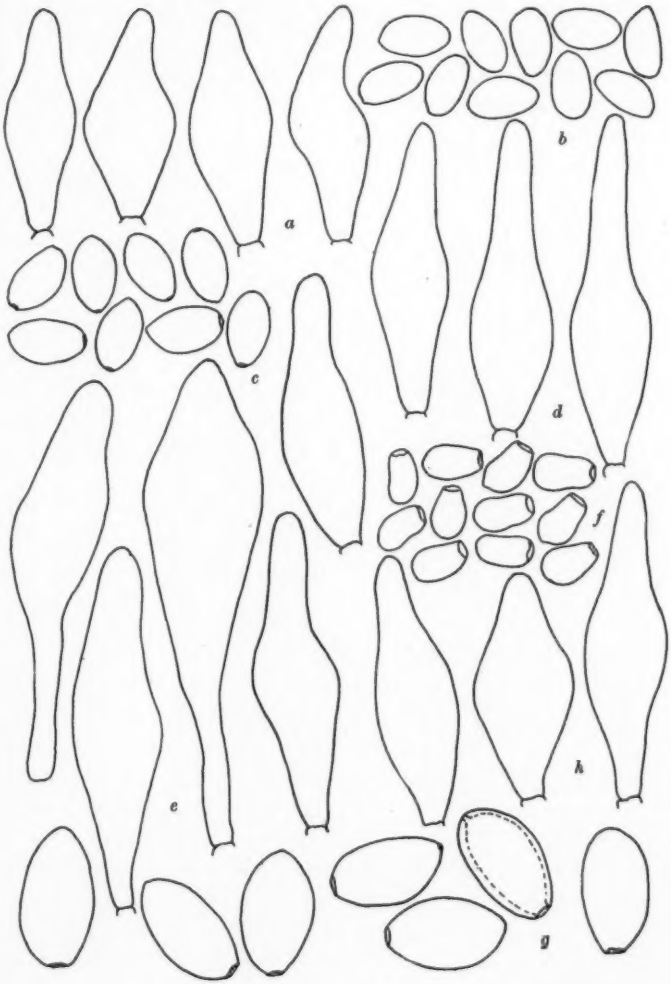


FIG. 1. *a, b, Psathyra microsperma; c, d, Psathyra multipedata; e, g, Psathyra umbonata; f, h, Hypholoma confertissimum.*

Arbor in 1905 by Kauffman and identified as *P. microsperma* by Peck himself. Kauffman first reported the species for Michigan using this collection as the basis of his report. During the past year I have had occasion to study the types of both *P. multipedata* and *P. microsperma* with the result that a critical review of all the species mentioned above has been made necessary.

Psathyra microsperma Peck (FIG. 1, *a, b*).—The type specimens of this species are rather badly broken up and not preserved in compact clusters. They give one the impression of a cespitose fungus in which the bases of the clusters are at best only loosely held together as in large bunches of *Hypholoma hydrophilum*. I found no evidence of a pseudorhiza. Due to the condition of the collection, however, the possibility that such a structure was present is not excluded. Pleurocystidia and cheilocystidia are similar and quite abundant. They measure 23–36 × 10–15 μ, and are tapered to a subacute apex above an inflated midportion. Their walls are thin and hyaline. The basidia are four-spored. The spores measure 6.5–8 × 4–4.5 μ, are ellipsoid, dull reddish-brown in dilute KOH under the microscope, and have a slightly flattened apex but *no distinct hyaline germ pore is visible under a 1.25 N.A. oil immersion lens*. The pileus-trama did not revive well, but appeared to have the layer of hyaline inflated cells over the surface which is characteristic of nearly all species of *Psathyra*.

The type of *Psathyra multipedata*, as Murrill (**3**) has pointed out, is in excellent condition. It consists of clusters of fruiting bodies, and a pseudorhiza projects from the base of the best preserved cluster. The microscopic characters are as follows: The spores measure 6.5–8 × 3.5–4 μ, are dull reddish-brown when mounted in dilute KOH, ellipsoid, and when viewed under an oil immersion lens are seen to be furnished with a *very distinct* hyaline apical germ pore giving the apex of the spore a truncate appearance. Pleurocystidia were found only near the edges of the lamellae and were similar to the cheilocystidia. The latter are very abundant and measure 35–46 × 9–13 μ. They are hyaline, narrowly fusoid with somewhat tapered apices, smooth, and have very thin walls. The pileus-trama is covered by a layer of somewhat elongated, inflated hyaline cells as previously illustrated, Smith (**7**). The cystidia and spores of the type are shown in figure 1, *c* and *d*.

Hypholoma confertissimum Atk. (FIG. 1, *f, h*).—This species was described in 1918 along with *H. comatum*. *Parker* (*5*) in his monograph of *Hypholoma* excluded *H. comatum* from the genus because he did not see the type. He failed to mention *H. confertissimum*. This situation is rather difficult to understand since the type specimens of both species can be readily located by their collection numbers in the Atkinson Herbarium at Cornell University. Atkinson suggested that *H. confertissimum* was related to *Hypholoma aggregatum* Peck. An examination of Atkinson's type also shows its relationship to *Psathyra multipedata* in the presence of a pseudorhiza and the characteristic cespitose habit which the species exhibits as a result. The microscopic characters of the species are as Atkinson briefly described them. In addition, I found the pileus-trama to be covered by a surface layer of hyaline inflated cells several cells deep. The pleurocystidia and cheilocystidia are abundant, 30–48 × 10–16 μ, and are narrowly to broadly fusoid with subacute apices. The spores are quite distinctive and serve to separate the species readily from both *H. aggregatum* and *P. multipedata*. They measure 5–6 × 3–3.5 μ and possess a hyaline apical germ pore which is much broader than in the spores of either of the other two. Figure 1, *f*, also shows a characteristic difference in shape.

In all of the Michigan collections identified as *P. microsperma*, including the one determined by Peck, the spores are furnished with a distinct hyaline germ pore. The cystidia are similar in shape and distribution to those of *P. multipedata*, but are readily located on the sides of the gills. The characteristic pseudorhiza of *P. multipedata* is present in my no. *33–1116* which was previously determined as *P. microsperma*. In Kauffman's material the manner in which the soil was cut away around the specimens prevents this character from being accurately determined. It is evident in one cluster, however, that not all of the base was obtained since the cut stems are visible underneath. Apparently his specimens were found growing in very hard compact soil.

If only the type specimens are considered, *P. microsperma* differs from *P. multipedata* in the spores which lack a characteristic hyaline germ pore when viewed under an oil immersion lens, in the more abundant pleurocystidia, and by the fragile nature of

the pileus as is evidenced by its failure to revive as well when sectioned and mounted in KOH. Macroscopically, according to the original descriptions, the former differs from the latter in having veil remnants at first scattered over the pileus, in the shorter stipes and apparently in the looser clusters formed by the fruiting bodies.

In my estimation the difference in the germ pore in the spores of the two species is sufficient to justify their recognition at least until a future study demonstrates that the character is not constant. Using this character as a starting point, all previously reported Michigan collections of *P. microsperma* should be classified under *P. multipedata*. The distribution of the pleurocystidia is a variable character in *P. multipedata*. I have studied abundant material (no. *33–1033; 5018; 5019*) from Michigan. In no. *5019* I first described them as absent whereas in no. *5018*, collected on the same day in a different locality they were present. These two collections were compared when fresh and found to be identical in every other respect. Later, when reexamining both collections in the herbarium a few cystidia were found on the gill faces of no. *5019*. Since the fruiting bodies of this species are exceedingly fragile, it did not seem wise to section from the type indiscriminately to see if a few pleurocystidia could be found scattered farther back from the edges of the gills. The observations cited above for the Michigan collections are regarded as sufficient evidence to establish the sporadic distribution of these organs in this species. The difference in the length of the cystidia of the two species is not, in my estimation, an important character. Obviously additional collections of *P. microsperma* are needed to properly characterize it. The length of the stipe, which Murrill emphasized, is likely to be variable, and the presence or absence of veil remnants is always troublesome. In regard to the pileus-trama, the manner in which the specimens were dried or their condition when collected could readily produce the difference noted. Kauffman (1) emphasized the word glabrescent in his description, which indicates to me that his specimens were already glabrous when collected, and does not raise an objection to their being placed in *P. multipedata*, which often has fibrillose remains of the veil scattered on the stipe.

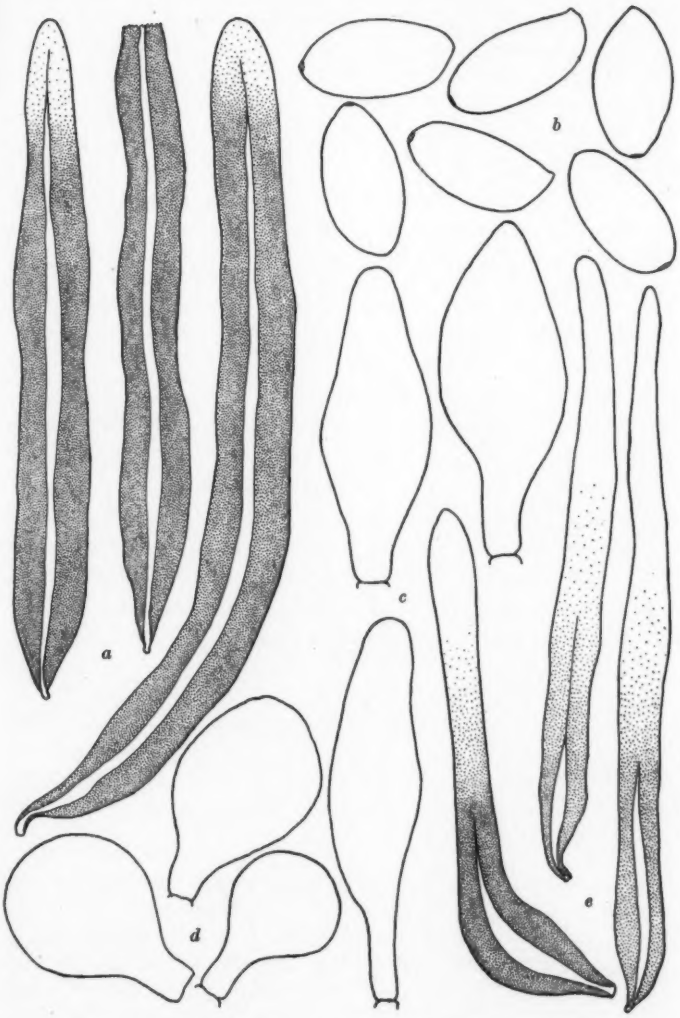


FIG. 2. *a–d, Psathyrella graciloides; e, Psathyrella gracillima.*

Psathyra stipitissima Lange is clearly a member of this group and can hardly be distinguished from *P. multipedata.* Lange described his species as lacking a veil, and with isodiametric-polygonate cells over the surface of the cap. He apparently described these cells from a surface view rather than from a vertical section through the pileus. He does not give information about the type of germ pore present in the spores. His comments, p. 11 (2), that " The densely stipitate growth distinguishes this species from all other Psathyras which individually bear some likeness to it " indicates that he had not considered any of the American species discussed here.

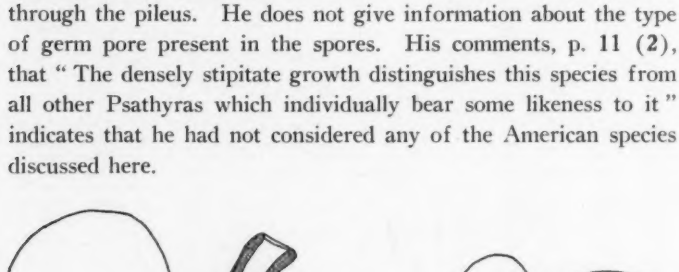


FIG. 3. *a, b, Psathyrella gracillima.*

The following description of *P. multipedata,* drawn from my notes, is given below to facilitate a comparison of it with both *P. stipitissima* and *P. microsperma*:

Pileus 1–4.5 cm. broad, ovoid to obtusely conic, becoming broadly umbonate, convex or nearly plane, surface glabrous, very young buttons (3 mm. ± broad) with a thin zone of white evanescent fibrils along the margin, smooth or at times regulose, hygrophanous, " Buckthorn Brown " over all and with a faintly striate margin when moist, lubricous, fading to whitish or dull lead gray along the margin and more or less " Ochraceous-Buff " on the disc; flesh thin and fragile, pallid, odor and taste not distinctive; lamellae close, narrow (3 mm. ±), ascending adnate, whitish, soon sordid purplish-brown, edge even and white fimbriate; stipe 5–10 cm.

long, 2–4 mm. thick, equal, hollow, very rigid and fragile, densely cespitose, the clusters branching from the apex of a long pseudorhiza which arises from a depth of a foot or more beneath the surface (The origin of this structure could not be traced due to mechanical difficulties, but it probably originates on deeply buried roots of elm and ash.), veil remnants slight and either scattered over the lower third of the stipe as white fibrillose flecs or forming a faint subbasal white fibrillose zone, upper two-thirds densely pruinose and often slightly striate; pileus-trama covered by a compact layer of vertically more or less elongated inflated cells; pleurocystidia varying from scattered in some pilei to rare or absent in others, 34–46 × 9–14 μ, narrowly flask-shaped; basidia four-spored; spores 6.5–8 × 3.5–4 μ, dark purplish-brown in water mounts when fresh, ellipsoid, with a distinct hyaline apical germ pore when viewed under an oil immersion lens.

Figure 4 illustrates the pseudorhiza and the type of cluster which results from this manner of growth. Very often three or four clusters occur very close together and the resulting compound cluster may contain over one hundred pilei. Smith (**7**), plate XX, illustrated unfaded pilei, and on plate XXI rugulose faded pilei. A comparison of figures 4 and 5 in this report shows at once the relationship between *H. confertissimum* and *P. multipedata*. Although the two species belong in the same genus, no new combination is justified until a revision of *Hypholoma, Psathyra, Psilocybe* and *Psathyrella* is completed.

PSATHYRA UMBONATA Peck (FIG. 1, *e, g*).

Pileus 1–4 cm. broad, obtusely conic to convex, becoming broadly convex or nearly plane, surface smooth to slightly rugulose, glabrous and moist, color variable, "Ochraceous-Tawny," "Cinnamon-Brown" or evenly "Tawny-Olive" except for the abruptly pallid margin when young, becoming "Dresden Brown," "Snuff Brown," "Sepia" or even "Olive-Brown" before fading, hygrophanous, "Pinkish-Buff," sordid "Cinnamon-Buff" or "Pale Olive-Buff" when faded (the umber colors of the moist cap develop as the spores mature); flesh thin, watery brown, fragile, odor and taste not distinctive; lamellae close but becoming subdistant, 18–22 reach the stipe, short ones in three tiers, bluntly adnate, broad (3–4.5 mm.), pallid to "Pinkish-Buff" when very young, becoming darker brown and finally "Fuscous" or with a purple sheen; stipe 5–8 cm. long, 1–2 mm. thick, strict and cartilaginous, tubular, equal, at first with scattered fibrils from the very rudimentary veil or veil entirely lacking, apex pruinose, soon

glabrous and polished, translucent in age and becoming sordid toward the base, base faintly mycelioid at times; spores 12–15 × 6.5–8 μ, ellipsoid with an apical hyaline pore, dark fuscous under the microscope; pleurocystidia rare to scattered, similar to cheilocystidia; cheilocystidia scattered to abundant 40–60 × 10–18 μ, inflated toward the middle and with obtuse apices, hyaline; basidia four-spored; pileus-trama corticated by an irregular layer of inflated cells, many of which have a short pedicel.

Scattered to gregarious on sticks and debris, Silver Lake, Dexter, Oct. 1, 1936 (No. *4991*), and Sept. 23, 1938 (No. *11042*). The spores of the type measure 12–15 × 6.5–8 μ, and possess an apical hyaline germ pore. The cheilocystidia are scattered, 40–60 × 10–12 μ, thin walled and hyaline. The pleurocystidia are present near the gill-edge and similar to the cheilocystidia. The pileus-trama did not revive well but isodiametric enlarged cells could be seen over the surface. No brown-walled setae were found. Kauffman's account of *P. umbonata* is erroneous. The two specimens in his collections, one obtained by him in 1906 and the other by Baxter in 1920, have the typical brown-walled setae on the surface of the pileus which characterize *Psathyrella subatrata,* and both answer the descriptions of that species in all other respects. Since Kauffman reported the species as infrequent it is logical to assume that he had seen it at least several times, but lacking additional specimens, it is impossible to evaluate his comments further.

PSATHYRELLA GRACILOIDES Peck (FIG. 2, *a, b, c, d*), and PSATHYRELLA GRACILLIMA Peck (FIG. 2, *e;* 3, *a, b*).

During the course of my study of *P. umbonata* and *Psathyrella subatrata,* I have had an opportunity to study the type specimens of *P. graciloides* and *P. gracillima* Peck. Peck's description and illustrations of the former are very suggestive of *P. subatrata.* The following data were obtained from a study of the type: The spores of *P. graciloides* measure 15–17 (18) × 6–8.5 μ, are ellipsoid, blackish under the microscope, and are furnished with an inconspicuous hyaline apical germ pore which gives to the apex a slightly flattened appearance. The basidia measure 22–24 × 10–12 μ and are four-spored. Pleurocystidia are present only near the edges of the lamellae and measure 35–50 × 10–16 μ. The cheilocystidia are of two types, either similar to the pleurocystidia

or much shorter and saccate, measuring 20–25 × 10–15 μ. The pileus-trama is covered by a surface layer of inflated hyaline cells which did not revive well enough in vertical sections of the pileus to allow their shape to be clearly discerned. In addition numerous setae with thick brown walls were scattered over the surface.

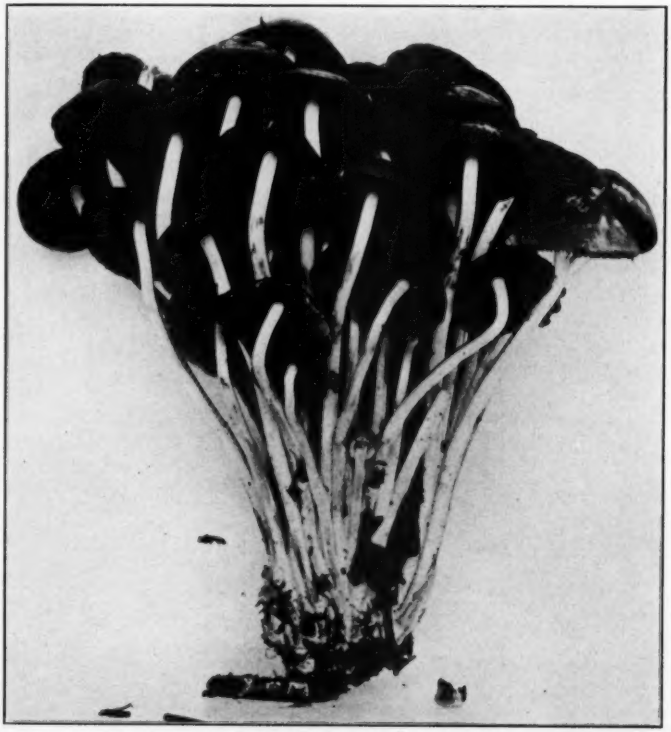


FIG. 4. *Psathyra multipedata* Peck × 1.

These measure 100 μ or more long and 4–6 μ thick. A comparison of Peck's type both macroscopically and microscopically with specimens of *Psathyrella subatrata* clearly shows that the two are the same. The matted fibrils referred to by Peck (**6** p. 43), are undoubtedly the brown-walled setae mentioned above. Peck's name is therefore to be regarded as a synonym of *P. subatrata.*

Apparently the relationship of *Psathyra conopilea* (Fries) Quél. to *Psathyrella subatrata* needs further study, see Lange (**2**).

Psathyrella gracillima Peck seems to be readily distinguishable from *P. subatrata* in its macroscopic characters. Its microscopic characters, however, are also very interesting. The pileus-trama is composed of very broad hyphae, and the surface is covered by a rather loose palisade of clavate cells which have pedicels fre-

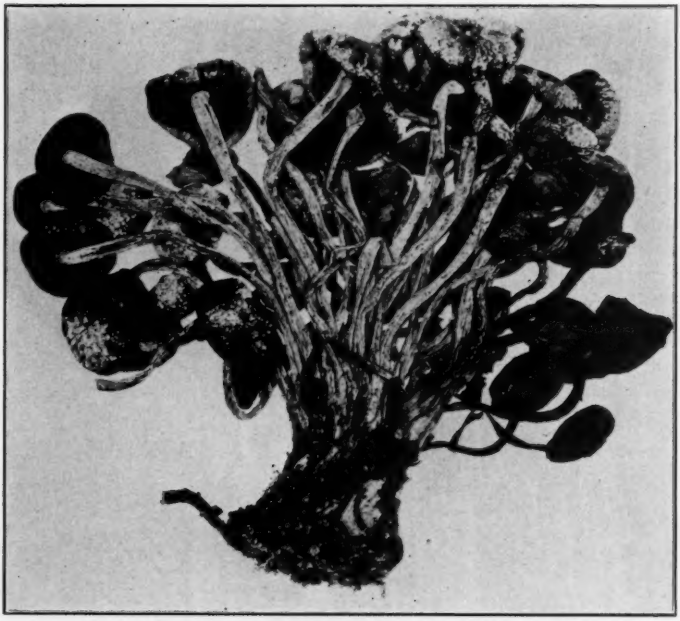


FIG. 5. *Hypholoma confertissimum* Atk. × 1. (Type)

quently furnished with brownish somewhat thickened walls. These cells measure 36–48 × 14–22 μ. In addition setae are also present. The latter arise from between the cells of the palisade, measure 80–150 × 4–7 μ, and are furnished with a thick-walled brownish base. The apical two thirds has more or less hyaline walls which are also thickened. The basidia are four-spored. The spores measure 12–14 × 7.5–9 μ, are coal-black under a microscope in KOH, and have a small apical hyaline germ pore.

No cystidia were seen. The hymenium is filled with very broad paraphyses as in species of *Coprinus*, and the manner in which the basidia with sterigmata are projecting is also strongly suggestive of that genus. The pilei of the type are plicate-striate and very delicate in texture.

FIG. 6. *Stropharia annelareiformis* × 1½.

STROPHARIA ANNELAREIFORMIS Murr (FIG. 6).

Pileus 1–3 cm. broad, obtusely conic, becoming campanulate and finally plane, sometimes slightly umbonate and the margin decurved, surface glabrous, viscid, margin faintly striatulate when moist, "Tawny" when young, becoming "Mars Brown," "Cinnamon

Brown" or "Verona Brown" when still moist, subhygrophanous and slowly becoming 'Buffy Brown" in age; flesh thickish, pallid, odor and taste not distinctive; lamellae close, broad, bluntly adnate with a decurrent tooth at times, seceding readily from the stipe, pallid to dull brown when young, finally becoming dark purple-brown, margin whitish and even; stipe 2–8 cm. long, 1–4 mm. thick, pallid tawny, rather coarsely pruinose above the annulus and decorated with fibrillose patches below which give it a whitish appearance at least when young, soon becoming hollow and in age the cavity rather large, often rooting in the manure, pseudorhiza up to 3–4 cm. long in some, base usually white mycelioid; annulus median or superior, membranous and flaring at first, often evanescent; basidia four-spored; spores 9–12 × 6–7.5 μ, with a hyaline apical germ pore, broadly ellipsoid in outline, obscurely angular, pale brown in KOH, dark purple-brown in mass; pleurocystidia not differentiated; cheilocystidia narrowly flasked-shaped to clavate, 25–30 × 6–12 μ, inconspicuous; pileus-trama homogeneous below a gelatinous pellicle.

Scattered on horse dung, Ann Arbor, July 1, 1933 (No. *33–571*). Murrill (**3**) reports it as known only from the type locality, New Orleans, La., but has recently listed it from Florida in a mimeographed list. My specimens differ from the species as he described it in the usually hollow stipe at maturity, the striate margin of the pileus, the lamellae not being truly decurrent, and in the presence of a rather well differentiated pseudorhiza in some specimens. Since Murrill described the species from rather meagre material and since my collection showed considerable variation in the characters just mentioned, it does not seem wise to describe the latter as a new species. The striations on the margin of the pileus often depend directly on the amount of moisture present in the trama, and since the colors as given by Murrill represent those of somewhat faded fruiting bodies in my collection, I am inclined not to place any significance on these differences. The attachment of the lamellae in *Stropharia* is also a variable character when one is comparing bluntly adnate gills which have a decurrent tooth with gills described as decurrent. The lamellae in broadly expanded pilei of species in which they are bluntly adnate often appear somewhat decurrent due to the way the gill-extremities are raised above a horizontal line. The attachment of the lamellae in Murrill's type appeared to be typical for coprophilous viscid species of *Stropharia*.

The presence of a pseudorhiza in some of my specimens presents a more serious difference, but in view of the small amount of material known, and the irregularity of the character in my collection, it can not be considered important at present. The microscopic characters of the type are identical with those given in the description.

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ANN ARBOR, MICH.

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DESCRIPTION OF FIGURES

The drawings of the cystidia, setae and spores were made with the aid of a camera lucida. The cystidia and setae are reproduced at a magnification of approximately 1250 ×. The spores are reproduced at a magnification of approximately 1500 ×. All of the illustrations were drawn from type specimens.

Fig. 1, *a* and *b*, pleurocystidia and spores of *Psathyra microsperma* Peck; *c* and *d*, spores and cheilocystidia of *Psathyra multipedata* Peck; *e* and *g*, pleurocystidia and spores of *Psathyra umbonata* Peck; and *f* and *h*, spores and cystidia of *Hypholoma confertissimum* Atk. Fig. 2, *a*, *b*, *c* and *d*, setae, spores, pleurocystidia and cheilocystidia of *Psathyrella graciloides* Peck; *e*, setae of *Psathyrella gracillima* Peck. Fig. 3, *a* and *b*, cells from the surface of the pileus and spores of *Psathyrella gracillima* Peck. Fig. 4, *Psathyra multipedata* Peck × 1. Fig. 5, *Hypholoma confertissimum* Atk. × 1 (type). Fig. 6, *Stropharia annellareiformis* Murr. × 1½.

RECLASSIFICATION OF CHYTRIDIUM SPINULOSUM WITH ADDITIONAL OBSERVATIONS ON ITS LIFE HISTORY

ALFRED F. BARTSCH

(WITH 24 FIGURES)

In the course of an examination of conjugating filaments of *Spirogyra Weberi* Czurda, collected in a roadside ditch near Seymour, Wisconsin, in the early summer of 1938, a rhizidiaceous fungus was found parasitizing the zygospores but not the vegetative cells. Because of its characteristic aculeated zoösporangia and its general habit of growth the organism was recognized as one described by Blytt in 1882 as *Chytridium spinulosum*. Study of the method of zoöspore discharge and the appearance of empty zoösporangia revealed that the apical structure, taken by Blytt to be an operculum of the *Chytridium* type, is actually an apical ornamentation similar in certain respects to the apical spine of *Obelidium*. It plays no part in zoöspore discharge since the spores escape through a sub-apical exit pore. On the basis of this difference it seems necessary to separate this species from *Chytridium* as the type of a new genus. The name *Blyttiomyces* is thus proposed in commemoration of the man who first collected this interesting fungus.

Since Blytt (**1882**) was unable to see zoöspore discharge in his material, he concluded from the general appearance and location of the sporangial apiculus that its function was that of an operculum. This, in addition to the intramatricality of the resting spores, led him to conclude that he was dealing with an undescribed species of *Chytridium*, and he accordingly described the chytrid under the binomial of *Chytridium spinulosum*. The present observations are not the first to show the inoperculate nature of the sporangium; it was recognized by Petersen (**1910**) since he described its dehiscence by a lateral orifice. It was also recognized later by Scherffel (**1926**) since he stated clearly that the apical

structure is not an operculum. In addition, he pointed out that the relationship of Blytt's fungus to *Chytridium* is doubtful. During the same year Denis (**1926**) described what he considered to be germinating resting spores, but his figure, however, suggests that he probably was dealing with mature zoösporangia and ungerminated resting spores in the same host. A brief description of this fungus was given by Cejp (**1932**). Although all the zoösporangia seen by him were empty, he was unable to find a lateral exit pore but did find a pore located near the apex of the sporangium. He did not see an operculum but maintained that the growth habit of the fungus indicated its systematic position in the genus *Chytridium*.

Blyttiomyces gen. nov.

Thalli partly intra- and extramatrical, monocentric, eucarpic. Zoösporangia extramatrical, globose, inoperculate, provided with an apiculus developing from distal portion of zoöspore case, with subapical exit pore; forming by enlargement of extramatrical spore and delimited from intramatrical portion of thallus by a septum. Zoöspores uniguttulate, uniflagellate. Intramatrical portion of thallus coarse, extensive, consisting of 2, rarely 3, apophyses, the distal one bearing a branched rhizoidal system. Resting spores intramatrical, variable in shape, forming by growth and encystment of an apophysis; germinating by the formation of an extramatrical sporangium liberating zoöspores.

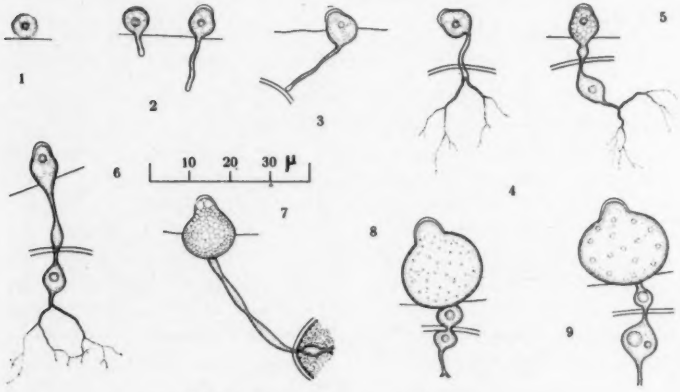
Thalli partim intra- et extramatricales, monocentrices, eucarpices. Zoosporangia extramatricalia, globosa, inoperculata, apiculata ex distale parte involucri zoösporae, cum exeunte poro subapicale; formantia augmento extramatricalis sporidii et de parte intramatricale thalli septo definita. Zoosporae uniguttulatae, uniflagellataeque. Pars intramatricalis thalli, crassa, lata, de 2 rare 3, apophysibus, distale ferente ordinem rhizoideam ramosamque. Quiescentia sporidia, intramatricalia, forma varia, formantia incremento encystmentoque apophysis; germinantia fabricatione extramatricalis sporangii zoosporas liberantis.

Blyttiomyces spinulosus (Blytt) comb. nov.

Chytridium spinulosum Blytt, Christiania Vidensk. Sellsk. Förh. p. 27. 1882 (no figures).

Zoösporangia multispored, aggregated, globose, inoperculate, hyaline, aculeated, 14.2–28.0 × 16.8–32.3, averaging 23.4 μ in diameter × 28.2 μ high exclusive of apiculus; with a single lateral exit pore about 40° from apex; aculei narrow, hyaline, about 0.5–

2.0 μ long, with rounded apices; apiculus cuculate, hyaline, smooth-walled, 5.6 μ in diameter $\times$ 3.5–4.9, averageing 3.8 μ high. Zoospores spherical to ovoid, hyaline, 4.2–7.0 μ in diameter, with a large, clear, refractive globule; flagellum approximately 25 μ long; zoöspore case becoming thickened distally, persisting as sporangial apiculus after germination. Intramatrical portion of thallus coarse, extensive; consisting of 2 tandem apophyses separated by zygospore wall of host, rarely with 3 apophyses, and with an extensive, branched rhizoid, up to 3.6 μ in diameter, extending from distal apophysis, tapering to delicate points. Apophyses spherical, ovoid or spindle-shaped, with smooth, hyaline membrane; proximal apophysis 5.6–7.0, averaging 5.9 μ in diameter, distal one 4.2–21.1,



FIGS. 1–9. *Blyttiomyces spinulosus.*

averaging 11.2 μ in diameter. Resting spores smooth, spherical, ovoid or irregular, 14.0–32.2, averaging 22.2 μ in diameter, with 2-layered, hyaline wall 3.0–5.0 μ thick; endospore 2.0–3.8 μ, exospore about 1.0–1.2 μ thick; with finely granular cytoplasm, containing 1 to several oleaginous-like globules; germinating by the formation of an extramatrical, aculeated sporangium lacking an apiculus; liberating zoöspores.

Zoosporangia multispora, aggregata, globosa, inoperculata, myalinula, aculeata, 14.2–28.0 $\times$ 16.8–32.3, circiter 23.4 μ in diametro $\times$ 28.2 μ in altitudine sine apiculo; cum exeunte poro in latere circiter 40° de apice; aculei angusti, hyalinuli, circiter 0.5–2.0 μ in longitudine, apicibus rotundis; apiculus cucullatus, hyalinulus, cum muris mollibus, 5.6 μ in diametro $\times$ 3.5–4.9, circiter 3.8 μ in altitudine. Zoosporae, sphaericae ad ovoideas, hyalinulae, 4.2–7.0 μ in diametro, cum magno claro globulo refracto; flagellum circiter 25 μ in longitudine; zoosporae vagina condensans distale, permanens apiculus spor-

angialus post germinationem. Pars intramatricalis thalli, crassa, ampla; cum 2 apophysibus muro zygosporiaco-hospitis separatis, rare cum 3 apophysibus, et cum amplo, ramoso rhizoid, ad 3.6 μ in diametro, ex apophyse distale, minuente ad apices molles. Apophyses sphaericae, ovoideae aut fusiformes, cum plana hyalinula membrana; apophysis proxima 5.6–7.0, circiter 5.9 μ in diametro, distalis 4.2–21.1, circiter 11.2 μ in diametro. Quiescentia sporidia plana, sphaerica, ovoidea aut inaequalia, 14.0–32.2, circiter 22.2 μ in diametro, cum muro hyalinulo, duorum ordinium 3.0–5.0 in crassitudine; endosporidium 2.0–3.8 μ, exosporidium circiter 1.0–1.2 μ in crassitudine; cum cytoplasma tenuiter granulosa, habente unum ad varios globulos oleaginos; germinante formatione sporangii extramatricalis aculeatique sine apiculo; liberante zoosporas.

Parasitic and saprophytic in the zygospores of *Spirogyra majuscula, S. Weberi,* and probably others; several parts of Europe and Seymour, Wisconsin.

DEVELOPMENT OF THE THALLUS

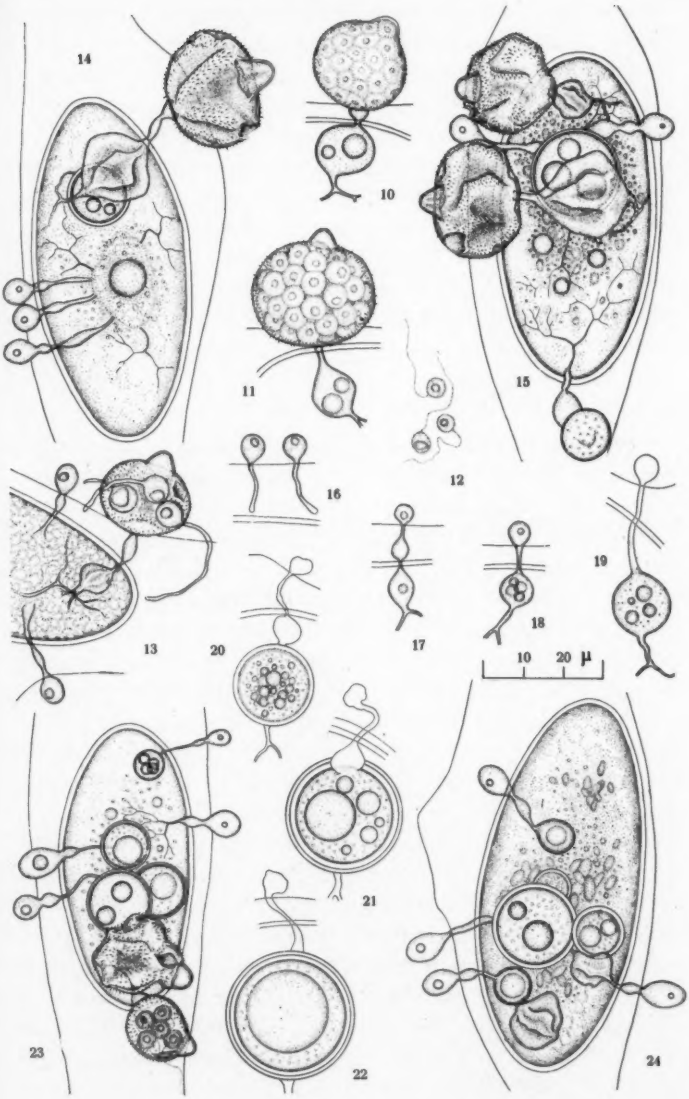
The zoöspores of *Blyttiomyces spinulosus* are spherical when at rest or slightly ovoid when in motion, hyaline, slightly vacuolated, 4.2–7.0 μ in diameter. Each contains a conspicuous, clear, spherical or irregular globule and a single posteriorly attached flagellum about 25 μ long (FIG. 12). Occasionally the globule is in a central position but in most zoöspores it is located near the anterior part of the cell. Locomotion is more or less uniform, occasionally rotational and is accompanied by feeble amoeboid movements when solid surfaces are contacted.

The zoöspores finally come to rest and germinate by sending out a delicate germ tube. Contact with a particular type of substratum is not a requisite for germination since some spores germinate free in the water. If the germ tube comes in contact with a host cell it penetrates the wall, and the young thallus utilizes the reserve food of the host for its continued growth. If no suitable host is reached by the growing tip of the germ tube, the young thallus does not develop further but disintegrates. The majority of thalli develop from zoöspores which germinate on the surface of the host cell.

The tip of the germ tube is bluntly rounded or inflated and is filled with hyaline cytoplasm; the cytoplasm back from the tip is more dense and slightly granular. Early growth apparently results from the absorption of water by the spore since the only

visible changes in its contents are the enlargement of the vacuoles already present and an increase in their number. The diameter of the germ tube at this stage varies from 1.5–3.0 μ with the greatest diameter at its tip (FIGS. 2, 3). The space between the host cell wall and the zygospore wall is rapidly traversed by growth of the germ tube until it comes into contact with the surface of the zygospore (FIG. 3). Contrary to the observations of Blytt (**1882**), no branching of the germ tube was seen before it penetrated the zygospore wall. A pore is next dissolved in the zygospore wall, and the tip of the germ tube grows into the interior of the zygospore and thus gains access to the reserve food of the host. It then grows into the protoplast and branches repeatedly.

A portion of the germ tube immediately inside the zygospore wall soon begins to enlarge as the anlage of an intramatrical subsporangial apophysis. An early stage in the formation of such a structure is shown in figure 4; here the enlarging portion is, as yet, hardly perceptible. Soon one or more refractive globules, similar to those of the zoöspores, appear in the cytoplasm of the enlarging apophysis (FIG. 5). When the size of the apophysis approaches that of the incipient extramatrical sporangium, the anlage of a secondary apophysis usually appears in the portion of the germ tube just outside the zygospore (FIGS. 5, 6). Its course of development, as a rule, is similar to that of the primary one, but usually it is smaller because of its delayed development (FIGS. 9, 10). However, exceptions to this relationship are not entirely lacking as shown in figures 8 and 15. In immature stages both show the same variations in shape; each begins as a vesicular, spindle-shaped swelling of the germ tube, and each becomes ovoid or spherical at maturity. Primary apophyses range from 4.2–21.1 μ in diameter, averaging 11.2 μ; secondary ones from 5.6–7.0 μ in diameter, averaging 5.9 μ. It is of interest to note that the size of the secondary apophyses is more constant than that of the primary ones. Several mature thalli were observed in which either one or both of the apophyses was absent, and one immature thallus was found in which two secondary apophyses were developing at the same time (FIG. 7). When they reach maturity two or three large globules are often present (FIGS. 9–11).



FIGS. 10–24. *Blyttiomyces spinulosus.*

Formation of the primary apophysis, beginning as it does at some distance from the point of origin of the first rhizoidal branches, precludes the occurrence of polyrhizoidal thalli. No thalli were observed which had extraneous rhizoids extending from various points on the surface of the apophysis as in certain species of *Entophlyctis*. The conditions conducive to or necessary for the formation of polyrhizoidal thalli has been well shown by Karling (**1931**).

The diameter of the rhizoids varies from 3.6 μ or more at the point of attachment to the apophysis to thinner delicate threads which taper to barely visible points at their extremities. Their contents, when visible, are irregularly granular and hyaline.

DEVELOPMENT OF THE ZOÖSPORANGIUM

Development of the zoösporangium is not delayed until the intramatrical parts of the thallus have reached their final size and absorptive capacity but begins at the time the zoöspore encysts on the surface of the host. Coincident with penetration by the germ tube, certain important and striking changes occur in the size, shape and detailed structure of the extramatrical spore body. Its distal hemisphere develops a thickened hyaline wall which gradually diminishes in thickness toward its equator (FIG. 2). This portion of the wall is the primordium of a future rigid, thick-walled, cucullate apiculus or ornamentation which will persist as such at the apex of the mature zoösporangium (FIGS. 11, 13–15, 23). Early development of this apiculus is fundamentally similar to the development of the apical spine in *Obelidium mucronatum* Nowakowski. Formation of the latter was described in detail by Sparrow (**1938**) who pointed out that the spine is set off early from the sporangium by the formation of a septum. In *Blyttiomyces*, however, the contents of the apiculus are confluent with those of the sporangium. Formation of the apiculus does not correspond to the development of an operculum of the *Chytridium* type since it was shown by Karling (**1936**) that the operculum in *Chytridium lagenaria* Schenck begins to form only after the sporangium has approached its mature proportions. That appears to be the usual course of development in operculate forms. Measurement of apicula on mature sporangia indicates that very little if any equatorial growth

follows the original thickening of the spore wall. As a result, enlargement of the incipient sporangium is confined to its proximal region; and the sporangium assumes a pyriform rather than a spherical shape (FIGS. 5–8).

The contents of the developing sporangium are finely granular and vacuolated. No refractive globules are visible, but during the succeeding growth stages numerous small ones make their appearance and increase in size until they resemble those of the zoöspores (FIG. 9). Accompanying these changes, the sporangium has attained mature size by translocation of material from the intramatrical portion of the thallus. During the final stages of enlargement the greater part of the contents of the apophysis flow more or less rapidly into the sporangium so that the former may finally contain only a few scattered granules and oil globules separated from the contents of the sporangium by a septum.

Mature zoösporangia are almost spherical or globose with an equatorial diameter slightly greater than the polar diameter exclusive of the apiculus (FIG. 10). They range from 14.2–28.0 μ in diameter $\times$ 16.8–32.3 μ high, averaging 23.4 μ in diameter $\times$ 28.2 μ high. The apicula range from 3.5–4.9 μ high, averaging 3.8 μ, and the average diameter at the base, which is almost constant, is 5.6 μ. As would be expected from its origin, the size of the apiculus is not proportional to the size of the sporangium upon which it is located but to the size of the zoöspore from which the thallus developed.

The contents of the sporangium are separated by cleavage furrows into a number of variable-sized portions, each of which encloses one of the refractive globules (FIG. 10). The cleavage portions are angular at first but soon become spherical and separated more or less from one another (FIG. 11). The refractive globule in each then appears quite prominent and similar to those of the free zoöspores (FIG. 12).

At the first indication of cleavage a striking change occurs in the nature of the sporangium wall which, until this time, has remained smooth over its entire surface. Numerous short hyaline projections appear on the surface of the sporangium exclusive of the apiculus, the latter remaining free of spines throughout the life of the thallus. The projections gradually elongate and become

more dense until they appear as opaque spines which give the sporangium an aculeated appearance at the time the zoöspores are mature (FIG. 11). They range from about 0.5–2.0 μ in length and are of uniform diameter with their tips bluntly rounded rather than pointed.

Casual observation of immature zoösporangia might lead one to believe, as did Blytt (**1882**), that the apical ornamentation is an operculum which separates from the sporangium and thus forms an opening through which the contents pass to the outside. However, when the zoöspores are ready for liberation, an orifice appears in the lateral wall of the sporangium about 40° from its apex (FIGS. 13–15, 23), and the apiculus plays no part in spore discharge, but remains in place. In the several zoösporangia in which spore discharge was seen, the exit pore appeared to be formed by deliquescence of a localized area of the wall. The pore thus formed later became jagged and irregular as if it were torn during exit of the spores (FIGS. 14, 15). In any event, the zoöspores escape individually through this orifice after having reached maturity; in no case observed were the contents extruded into a thin-walled vescicle as described by Scherffel (**1926**). After passing into the water the zoöspores pause momentarily and then move quickly away.

In exceptional cases all the zoöspores may not escape through the sub-apical pore as described but may remain inside and germinate. The resulting germ tubes either project through the exit pore or penetrate through the sporangium wall. In one such case three spores sent their germ tubes through the wall of the sporangium, two penetrated the host cell wall, and one of them had almost contacted the surface of the original zygospore (FIG. 13). The refractive globule apparently is used as food during the early stages of development since the size of the globule in each of the germinating spores was inversely proportional to the length of its germ tube. Such spores were never observed to send their germ tube into the host cell through the old germ tube and apophysis of the original sporangium as in *Phlyctochytrium chaetiferum* Karling (Karling, **1937**). Among other abnormal phenomena were several sporangia which had developed between the two walls of the host. When zoöspores were liberated from such sporangia, they

had no exit to the outside and consequently germinated free in the lumen of the cell or in contact with the surface of the zygospore.

DEVELOPMENT OF THE RESTING SPORE

Resting spores are formed in abundance during later stages of infection after most of the reserve food of the zygospore has been utilized by the fungal thalli. Although generally but 3 or 4 are formed in a single zygospore (FIGS. 23, 24), as many as 7 have been observed in the present material, Petersen (**1910**) figured 14, and Cejp (**1932**) has photographed as many as 12. This difference in the number of resting spores per zygospore may be related to the different host species involved in the different collections.

Only one resting spore is formed from a single thallus, and the process of formation involves enlargement, accumulation of reserve food and encystment of the primary apophysis (FIGS. 16–22). Early stages in development of thalli which will form resting spores are similar in certain respects to those of thalli which form zoösporangia. The most obvious difference is the failure of the zoöspore wall to thicken to the same degree as in the zoosporangial thalli (FIG. 16). Shortly after the first rhizoidal branches have been established, the anlage of a prominent primary apophysis appears and enlarges rapidly. Its size and shape are similar to those previously described, but here the apophysis soon becomes spherical (FIG. 18, 19). This type of growth is distinctly endogenous and is similar to that of *Chytridium*. Oleaginous-like globules appear, and their substance will persist in the mature resting spore where it probably will serve as reserve food during germination. The contents of the germ tube and rhizoidal system apparently become incorporated into the resting spore because they soon appear empty and somewhat collapsed. The presence of a hyaline periphery on the apophysis at a slightly later stage (FIG. 20) indicates that a thickened wall is being laid down about the developing spore. This soon destroys communication with the rhizoidal system at one pole and with the germ tube at the other. An increase in the size of the globules, accompanied by a decrease in their number, indicates that they probably begin to

coalesce at this time. As the resting spore approaches maturity, the wall becomes differentiated into two layers, and no further size increase occurs. The inner layer, or endospore, of the wall is usually thicker and more hyaline than the exospore. In all the material we have examined there were no rugose resting spores as described by Cejp (**1932**). Secondary apophyses occur only occasionally in these thalli, and rarely two apophyses may form inside the zygospore (FIGS. 20, 21). Further coalescence of the refractive globules may or may not occur so that some mature spores contain a single large globule that fills almost the entire cell (FIG. 22) while others contain a number of them suspended in the protoplasm (FIG. 21).

Mature resting spores are usually smooth-walled spherical, ovoid or sometimes irregular depending upon their number, size and location in the zygospore. They range from 14.0–32.2 μ in diameter, averaging 22.2 μ. The wall ranges from 3.0–5.0 μ in thickness, the endospore from about 2.0–3.8 μ and the exospore from about 1.0–1.2 μ. If a single refractive globule is present, it is usually eccentric in position (FIG. 22).

Only a few resting spores were observed to germinate but our observations agree with those of Petersen (**1910**), Blytt (**1882**), Denis (**1926**) and Cejp (**1932**). The final result of resting spore germination is the formation of an extramatrical sporangium which liberates zoöspores. Blytt (**1882**) and Cejp (**1932**) described the resting spore as sending a germ tube to the surface of the host where its tip enlarges to form a sporangium. It was impossible in the present material to determine whether the contents of the resting spore pass out into the old zoöspore case as in the germination of resting spores of *Chytridium lagenaria* (Karling, **1936**) or whether new germ tubes are sent out to the surface of the host as reported by Blytt (**1882**) and Cejp (**1932**). It is possible that both methods occur under appropriate conditions. Several stages in resting spore germination are shown in figures 23 and 24. Discharge of zoöspores from resting sporangia was not observed, but the characteristics of a single empty one are the same as those described by Blytt (**1882**). He found that the sporangium is small and spiny-walled and lacks an apiculus. Absence of the apiculus is not surprising in view of the fact that the

wall of the old spore undergoes no unequal thickening and because resting sporangia may possibly form by enlargement of the tips of new germ tubes. The exit pore on this sporangium also was located about 40° from the apex and in this character was similar to the zoösporangia.

Blytt (**1882**) reported that in some cases the resting spores are formed by a process of copulation since he observed only one half as many resting spores as the number of thalli which had formed. In addition he saw what he considered to be empty haustoria which had fused with others. In the present material no such copulation was seen, nor did there appear to be any type of sexual process involved in the formation of resting spores. His observation that the number of resting spores does not correspond with the number of thalli is not significant since zoösporangial thalli do not form resting spores and are actually empty in later stages. It is also possible that Blytt was dealing with several different fungi in the same host.

DISCUSSION

That this fungus is capable of parasitic growth is shown by its infection of *Spirogyra* zygospores which apparently are living and in a normal healthy condition. It is also capable of saprophytic nutrition since numerous infections occur on zygospores which have been depleted of food by other thalli (FIG. 14). The lethal effect upon the host is almost immediate following establishment of the rhizoidal system, and this is manifested by the breakdown of the chloroplasts and the appearance of oil globules. Later on, the only remains of the zygospore contents are a few scattered granules which appear to be broken down pyrenoids (FIG. 24) or several oil globules of different sizes mingled with numerous smaller granules (FIGS. 15, 23). The enzymatic activity of the rhizoidal system seems to have little if any effect upon the zygospore wall. In this respect it is strikingly different from the thallus of *Lagenidium americanum* Atkinson, also an inhabitant of *Spirogyra* zygospores, which uses up or at least destroys the wall completely.

The host range of *Blyttiomyces spinulosus* is apparently quite restricted and has been reported only from species of *Spirogyra*.

The species of *Spirogyra* were not determined for the collections of Blytt (**1882**) from Norway, of Petersen (**1910**) from Denmark, of Scherffel (**1926**) from Slovakia, nor Cejp (**1932**) from Slovakia. Denis (**1926**) believed the host he collected from France to be *S. majuscula* Kützing. The reports of this fungus only from species of *Spirogyra* indicates that it probably is restricted to this genus.

In considering the relationship of *Blyttiomyces* to other genera of the Rhizidiaceae it becomes apparent at once that its affinities point to the genus *Chytridium*. The occurrence of an operculum-like structure on the apex of the zoösporangium might lead one to conclude that the former is virtually the relic of a pre-existing operculum which has lost its function after the establishment of an exit pore method of zoöspore discharge. That this is unlikely is shown by a comparison of its formation with that of a typical operculum as found in *Chytridium* (Karling, **1936**), in *Endochytrium* (Sparrow, **1933**; Karling, **1938**), and *Nowakowskiella* (Sparrow, **1933**). In these genera the operculum does not form until the zoösporangium has attained almost its mature proportions, and it has no anlage which develops from a distinct part of the zoöspore. The general habit of growth, the formation of intramatrical resting spores, and the method by which they germinate shows clearly a close relationship between this fungus and *Chytridium*.

ACKNOWLEDGMENTS

This investigation was carried out under the direction of Dr. E. M. Gilbert during the tenure of an Alumni Research Assistantship by the writer. Many helpful suggestions and pertinent information were also given by Dr. F. K. Sparrow, Jr., of the University of Michigan, and the Latin diagnoses were written by Mrs. N. E. Stevens of Champaign, Illinois. The writer wishes to express his appreciation of their willing assistance.

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EXPLANATION OF FIGURES

All figures were drawn with the aid of an Abbe camera lucida, using a 10 × ocular and 1.8 mm. objective; original magnification of figures is 1600 ×.

Fig. 1. Zoöspore resting on surface of host; 2, elongation of germ tube in direction of host zygospore; 3, germ tube in contact with zygospore wall; 4, early stage in formation of rhizoidal system (note incipient sporangium beginning to enlarge and take on pyriform shape); 5–6, early development of primary and secondary apophyses containing refractive globule; 7, abnormal specimen forming 2 secondary apophyses; 8–11, enlargement of zoösporangium and formation of zoöspores; 12, zoöspores after liberation from sporangium; 13, sporangium with 3 germinating zoöspores (note that 2 germ tubes have penetrated host cell wall and are growing toward original host zygospore); 14–15, zygospores of *Spirogyra* with young thalli, empty zoösporangia showing location of exit pore, and 2 resting spores; 16–21, stages in development of resting spore; 22, resting spore with single large globule; 23–24, *Spirogyra* zygospores with young thallus, resting spores, germinating resting spores, and one sporangium liberating zoöspores.

STUDIES ON THE USTILAGINALES OF THE WORLD [1]

GEORGE L. ZUNDEL

(WITH 3 FIGURES)

The purpose of this paper is to record the results of studies on specimens of Ustilaginales received from various countries of the world. One new genus and fifteen new species are recorded.

I. NOTES ON SMUTS REPORTED ON CYNODON DACTYLON (L.) PERS.

In 1847 Tulasne [2] reported *Cynodon Dactylon* as a host plant for *Ustilago Carbo*. Later in 1870 Passerini [3] described and issued this smut in exsiccati as *Ustilago Carbo* Tul. *β Cynodontis* Pass. P. Hennings [4] in 1891, based on a collection by G. Schweinfurth in Erythrea, used the name *Ustilago segetum* (Bull.) Dittm. var. *Cynodontis* P. Henn. In present day literature this smut is now usually referred to as *Ustilago Cynodontis* P. Henn. However, in 1927 Curzi [5] correctly suggested that the name should be written *Ustilago Cynodontis* (Pass.) Czi. The name *Ustilago Cynodontis* P. Henn.[6] was not published till 1893.

Another smut was described by Tulasne [7] in 1847 based on a collection at the Cape of Good Hope and deposited in the Drege Herbarium (no. *9467*) as *Ustilago Dregeana* Tul. but no host was given. Nothwithstanding the excellent article by P. Magnus [8] in which all of the species of smuts on *Cynodon Dactylon* are carefully differentiated, these species have been confused in later

[1] The Latin diagnoses of new species were written by Dr. R. E. Dengler of the Pennsylvania State College, to whom the author expresses his appreciation and thanks.

[2] Ann. Sci. Nat. III. **7**: 82. 1847.

[3] Erb. Critt. Ital. II. no. 450. 1870.

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[6] Bull. Herb. Boiss. **1**: 144. 1893.

[7] l.c. p. 83.

[8] Les Ustilaginees du *Cynodon Dactylon* (L.) et leur distribution geographique. Bull. Soc. Myc. Fr. **15**: 265–271. 1899. *ill.*

literature. Even as late as 1927, Verwoerd [9] considered *Ustilago Cynodontis* P. Henn. as a synonym of *Ustilago Dregeana* Tul. The confusion apparently began in 1882 when von Thumen reported [10] *Ustilago Dregeana* Tul. on *Cynodon Dactylon,* based on a collection by MacOwan in East Africa. Later in Saccardo's Sylloge Fungorum [11] the habitat of *U. Dregeana* is reported as "inflorescence graminis in *C. Bonae* Spei (Drege) & Cynodontis Dactyli, Somerset East Africa (MacOwan)."

In order to further emphasize the difference between these species, the writer has been able to secure parts of original collections and reëxamine them.

Collections of *Ustilago Cynodontis* P. Henn. from Australia, Siberia, Texas and Tunis were examined under high power. In all cases the spores were chiefly globose, olivaceous brown and smooth, averaging 7 μ in diameter (FIG. 1*A*).

Through the courtesy of the Director of the Royal Botanical Garden, Kew, England, some spores of the MacOwan collection, marked *Ustilago Dregeana,* were secured. An examination showed that they agreed perfectly with those of *Ustilago Cynodontis* P. Henn. (now *Ustilago Cynodontis* (Pass.) Czi.).

A portion of the type of *Ustilago Dregeana* Tul. was secured from the Laboratoire de Cryptogamie of the Museum National d' Histoire Naturelle in Paris through the courtesy of Dr. Roger Heim. An examination of this material showed that the spores were reddish-brown, with a dark thick epispore and under high magnification were papillate to warty, 4–5 μ diam (FIG. 1*B*). From the illustrations of the spores of *U. Cynodontis* and *U. Dregeana* one wonders how the two species were ever confused.

It must be noted that in the original Tulasne description of *Ustilago Dregeana* no host was given. It merely says "Gramen morbosum in Herbario Dregeana (no. *9467*)" etc. In an attempt to find the name of the host, a portion of the type specimen of *U. Dregeana* was sent to Mrs. Agnes Chase of the U. S. Dept. of Agriculture for her opinion. Under date of May 27, 1937, she reports in part as follows: "This host is certainly not a species of

[9] Ann. Univ. Stellenbosch A. **4**: 19. 1926.
[10] Grevillea **9**: 18. 1882–1883.
[11] Sacc. Syll. Fung. **7**: 467. 1888.

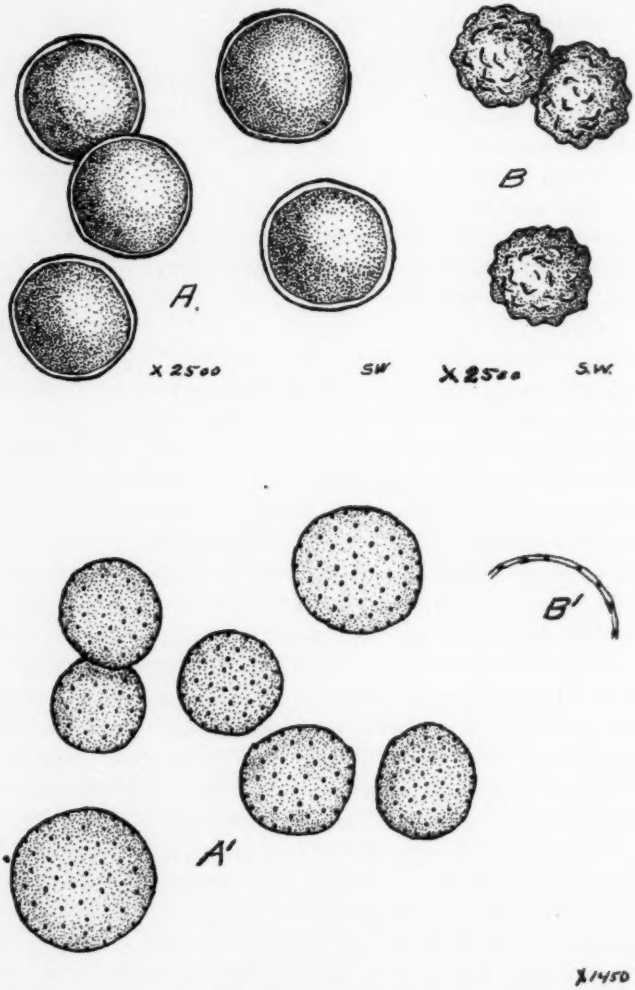

FIG. 1. *A*, spores of *Ustilago Cynodontis* P. Henn.; *B*, spores of *Ustilago Dregeana* Tul. (type); *A'*, spores of *Ustilago paraguariensis* Speg.; *B'*, section of epispore.

Cynodon. I feel confident that it is a species of *Eragrostis.* I have been through all the African material to compare with your specimen. There is practically nothing to go by except the hairs at the summit of the sheath. There are some ten or twelve species of Africa that have hairs much like this. Of these, three are common in the region of the Cape, where Drege collected, and of these three, *Eragrostis porosa* Nees, I think, matches your specimen fairly well." This then seems to be proof that the two species of smuts do not even occur on the same host plant.

Another species on *Cynodon Dactylon* was described by Spegazzini from Paraguay, which he named *Ustilago paraguariensis.*[12] This species is said to differ from *U. Cynodontis* P. Henn. by the larger spores which are granular to echinulate. In the article by P. Magnus,[8] already referred to, the spores of these two species are pictured and the distinctions noted. Curzi,[5] in the above mentioned article, considers *U. paraguariensis* Speg. a synonym of *U. Cynodontis.* Original exsiccati specimens of *U. paraguariensis* Speg. have been examined and found to not agree in spore markings with *U. Cynodontis,* but do agree in size of spores, averaging 10.5 μ in diam.

Spores of *U. paraguariensis* Speg. from Roumeguere Fungi Sel. Exs. no *4113,* collected at Balansa, the type locality, from the Farlow Herbarium were examined, and under oil immersion the spores are olivaceous brown with thickened or punctate areas in the epispore which at first suggest echinulations (FIG. *2A*), and average 10.5 in diam. The thickenings in the wall are shown in figure *2B.*

Spores of *U. paraguariensis* from a second collection from the exsiccati collection of the Connecticut Agricultural Experiment Station (no. *1322,* Vest. Micr. Rar. Sel) were examined under oil immersion, and were found to be olivaceous brown, indistinctly granular, averaging 10.5 μ diam. There seems to be no question but that *U. Cynodontis* P. Henn. and *U. paraguariensis* Speg. are distinct species. In *U. paraguariensis* Speg. the granular thickenings are visible only under oil immersion. The spores appear smooth when examined under low magnification.

[12] Anal. Soc. Ci. Argent. **17**: 89. 1884.

II. A NEW GENUS OF THE USTILAGINALES FROM SOUTH AFRICA

Xylosorium Zundel, gen. nov.

Sori as oval pustules on the stem, 3–4 septate, covered with a hard spony coriaceus membrane which ruptures irregularly at maturity disclosing a dark brown semi-agglutinated spore mass; spore-balls composed of many fertile spores which usually disintegrates into single spores at maturity.

Germination not known.

Type species, *Xylosorium Piperii* Zundel.

Soris in stirpe pustulis ovalibus, 3–4 septatis, membrana dura spongiosa coriaceaque tectis, membrana matura irregulariter rupta massam atro-brunneam et semi-agglutinatam sporarum detegit; globulis sporarum exmultis et fertilibus sporis compositis in singulasque sporas mature disintegratis. Germinatio non cognoscitur.

Xylosorium Piperii Zundel, sp. nov.

Sori as hard coriaceus, oval pustules on the stem, 1.5 to 2 mm. in diam., 3 to 4 septate, at maturity rupturing irregularly on the upper side of the sorus, spore mass dark brown, semi-agglutinated but later becoming powdery; spore-balls many spored, broadly ellipsoidal, opaque, dark colored, semi-permanent, chiefly 77 to 115 μ long; spores globose to ellipsoidal, often angled by compression, light olivaceous-brown, smooth, somewhat zonate under high magnification, 7–10.5 μ long.

Soris duris coriaceis, ovalibus pustulis in stirpe, 1.5–2 mm. diam., 3–4 septatis, maturis irregulariter supra in soris ruptis, massa sporarum atro-brunnea, primo semi-agglutinata postea pulverulenta; globis multas sporas habentibus, late ellipsoideis, opacis, fuscis, semi-permanentibus, plerumque 77–115 μ longis; sporis globosis vel ellipsoideis, saepe per compressionem angulatis, sub-olivaceo-brunneis, levibus, aliquantum zonatis "sub oleo," 7–10.5 μ longis.

On *Piper* sp., Transvaal, Union of South Africa, collected by Archdeacon Rogers, Nov. 1915 (Union Dept. Agr. Myc. Herb. No. *11806*) (FIG. 2).

This peculiar smut is one of the few species ever reported on woody plants. It was with difficulty that the writer convinced himself that it was a member of the Ustilaginales. The spores are apparently too old to germinate but the genus is temporarily included in the Ustilaginaceae until fresh material is collected and the spores germinated (FIG. 2).

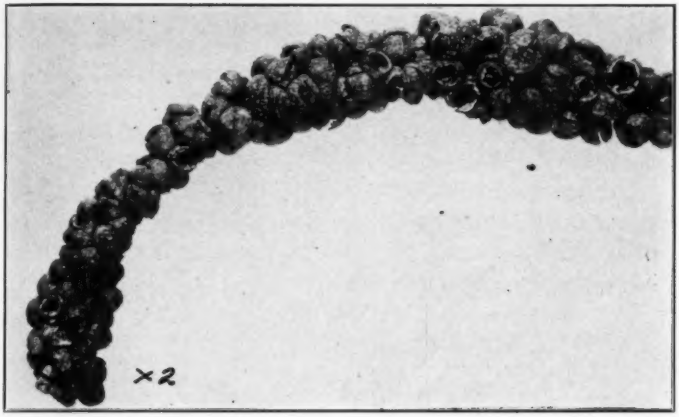

FIG. 2. *Xylosorium Piperii* Zundel.

III. SMUTS COLLECTED IN COLUMBIA BY C. E. CHARDON

The following smuts were sent to the writer by Dr. H. H. Whetzel of Cornell University and have been determined as follows:

Cintractia caricis (Pers.) Magn. on *Carex Boudplanii* Kunth., Teguendama, Dec. 13, 1938 (no. *872*), and Penanegra above Facatotiva, March 28, 1937 (no. *864*); *Carex chordalis* Liebm., Teguendama, Dec. 13, 1936 (no. *870*); *Farysia olivacea* (DC.) Sydow, on *Carex Haenkeana* Presl, swampy ditches near Facatotiva, March 28, 1937 (no. *863*); *Sphacelotheca borealis* (Clint.) Schell, on *Polygonum punctatum* Ellis, La Virginia, Camine del Buiz, Dec. 25, 1936 (no. *865*); *Urocystis anemones* (Pers.) Wint. on *Ranunculus* sp., La Laguna, Paramos del Buiz, Dec. 27, 1936 (no. *871*); *Ustilago Hordei* (Pers.) Kellerm & Swingle, on *Hordeum vulgare* L., outskirts of Bogota, March 7, 1937.

IV. SMUTS COLLECTED IN MINAS GERAES, BRAZIL BY A. S. MÜLLER

The following smuts were sent to the writer by Dr. H. H. Whetzel of Cornell University for determination.

Entyloma Oryzae Sydow, on *Oryza sativa* L. var. Honduras, Viçosa, Escola, March 20, 1930 (no. *1011*).

Mykosyrinx Cissi (DC.) Beck, on *Cissus sicyoides* L., Viçosa, May 27, 1930 (no. *177*).

Sorosporium reilianum (Kuhn) McAlpine, on *Zea Mays* L., Viçosa, Escola, May 16, 1933 (no. *534*).

Sphacelotheca cruenta (Kuhn) Potter, on *Sorghum vulgare* Pers. (*Holcus sorghum* L.) (sorgo), Vicosa-Escola, May 19, 1932 (no. *344*).

Sphacelotheca culmiperda (Schroet.) Clint., on *Andropogon bicornis* L., Vicosa, Feb. 25, 1934 (no. *739*).

Sphacelotheca bicornis (P. Henn.) Zundel, on *Andropogon bicornis* L., Uberlandia, May 19, 1936 (no. *1082*), also Vicosa-Escola, March 20, 1932 (no. *322*).

Tilletia rugispora Ellis, on *Paspalum plicatum* Michx., Curvello, Feb. 1, 1936 (no. *1010*).

Tolyposporium Cenchri Bref., on *Cenchrus echinatus* L., Rio Branco, July 31, 1934 (no. *828*).

Ustilago Avenae (Pers.) Jens. on *Avena sativa*, Vicosa-Escola, Feb. 20, 1930 (no. *619*).

Ustilago gregaria Zundel, on *Panicum rivulare Trin.*, Barrosa, Feb. 18, 1934 (no. *710*).

Ustilago Schroeteriana P. Henn., on *Panicum Urvillei* Steud., Vicosa-Escola, Dec. 1, 1929 (no. *69*).

Ustilago Tritici (Pers.) Rostr. on *Triticum vulgare* L., Vicosa-Escola, Feb. 3, 1930 (no. *99*); also Dec. 7, 1933 (no. *646*).

Ustilago Zeae (Beck.) Ung., on *Zea Mays*, Vicosa-Escola, March 12, 1931 (no. *316*); on *Euchlaena mexicana* Schrad, Escola-Vicosa, March 20, 1932 (no. *318*).

V. SOUTH AMERICAN SMUTS FROM THE FARLOW HERBARIUM, HARVARD UNIVERSITY

Cintractia leucoderma (Berk.) P. Henn., on *Rhynchospora aurea*, Pl. Vryheid, British Guiana, coll. D. H. Linder (no. *942*), Feb. 14, 1924.

Cintractia utriculicola (P. Henn.) Clinton, on *Rhynchospora corymbosa* (L.) Brit., Pl. Vryheid, British Guiana, coll. D. H. Linder (no. *941*), Feb. 14, 1924.

Entyloma australe Speg., on *Physalis* sp., Buenos Aires, Argentina, coll. Roland Thaxter (acc. no. *7893*), 1905–'06.

Ustilago bromivora (Tul.) Fisch. de Wald., on *Bromus catharticus* Vahl., El Prado, Motevideo, Uruguay, coll. R. Thaxter, Oct. 22, 1905 (acc. no. *7896*), also near St. Catharina, Agricultural School, Argentina, March 25, 1906, coll. R. Thaxter (acc. no. *7900*).

Ustilago minima Arth. on *Stipa hyalina* Nees, Montevideo, Uruguay, coll. R. Thaxter, Oct. 22, 1905 (acc. no. *7894*).

Ustilago Rabenhorstiana Kuhn, on *Digitaria* sp.? Buenos Aires, Argentina, coll. R. Thaxter, Oct. 1905 (acc. no. *7897*).

Ustilago Thaxteri Zundel, sp. nov.

Sori destroying the inflorescence, extending down and surrounding the upper portions of the stems, at first partially hidden by the sheaths, 10 cm. or more in length, at first covered by a whitish delicate membrane of host tissue which flakes away revealing a semi-agglutinated spore mass, later becoming dusty, surrounding the inflorescence and stems; spores light olivaceous-brown, chiefly subspheric, somewhat irregular, smooth, often guttulate, chiefly 8–12 μ in length.

Soris infloresentiam destruentibus, descendentibus et superior caulium cinogentibus, primo partim in vaginia celatis, 10 cm. vel amplius longis, subalba et delicata membrana primo tegatis; membrana postea in laminae rupta semi-agglutinstam sporarum massam detegit; membra postea pulverulenta facta caulis circumstat; sporis sub-oliveo-brunneis, plerumque subspericis, irregularibus, levibus, saepe gutulatis, plerumque 8–12 μ longis.

On *Leptochloa uninervia* (Presl.) Hitch. & Chase, Buenos Aires, Argentina, coll. Roland Thaxter, Sept. 29, 1905 (Farlow Herb. acc. no. *7899*, type); Sept. 29, 1905 (Farlow Herb. acc. no. *7909*); Oct. 8, 1905 (Farlow Herb. acc. no. *7911*).

VI. NOTES ON USTILAGO CARBO γ COLUMELLIFERA TUL

In 1847, Tulasne[13] published the name *Ustilago Carbo* γ *columellifera* and described two varieties as follows:

γ *columellifera:* gleba ustilaginea definita, ovarii locum tenens, columellam simplicem vel ramoso-spinescentem includens, bracteis propioribus liberis vel ipsi partim adnatis; sporis diametro 0mm, 0096–0128 crassis, saturiatuis coloratis.

a. transfissa.—Mole ustilaginea ovarum mentiente, centrali et plane libera; columella simplici. (In *Andropogo hirto.*)

b. trichophora.—Mole ustilaginea bracteis hinc pro parte adnata, columella ramoso-spinescente. (In Panico Colonum, *Penniseto cenchroide.*)

[13] Ann. Sci. Nat. III. 7: 81. 1847.

In using the name *Ustilago Carbo,* Tulasne was merely correcting nomenclature since DeCandolle had used the name *Ustilago Carbo* [14] in 1815 to include many of the cereal smuts, however, *Ustilago Carbo* Tul. included more than the cereal smuts.

In his two most extensive publications Fischer de Waldheim [15, 16] simply uses the name *Ustilago Carbo* Tul. with spores 6–8 micr. and lists from eleven to eighteen unrelated hosts for this smut, including the cereals and several grasses such as *Andropogon hirtus* L., *Cynodon Dactylon* Pers. but not *Pennisetum* sp. or *Panicum* sp.

In his second paper Fischer de Waldheim [17] recognizes the name *Ustilago Penniseti* Rabh. with spores 10–12.4 micr. and uses as a synonym *Ustilago Carbo* var. *columellifera* β *trichophora* Tul.

As to the other variety of *Ustilago Carbo,* the writer has found it only once since the original publication. Oudemans [18] lists *Ustilago segetum* (Bull.) Ditm. on *Andropogon hirtus* L. and gives as a synonym *Ustilago Carbo* γ *columellifera* a. *transfissa.*

Other writers have considered these smuts differently. In 1910, McAlpine [19] obtained a smut specimen labeled "*Ustilago Carbo* var. *columellifera* Tul." which he studied and concluded that it was a *Cintractia* and published the name *Cintractia columellifera* (Tul.) McAlp. with spores 7–8 μ diameter.

In 1928, Ciferri [20] published the name *Sphacelotheca columellifera* (Tul.) Ciferri but did not give a description so that one does not know the source of his material nor why the change in nomenclature was made. In 1930, the writer [21] published a description, presumably of the Tulasne species, using the name proposed by Ciferri. As material an Australian specimen was used which had been sent from the New South Wales Department, Biological Branch, No. 8A, and labeled "*Cintractia columellifera* on *Andropogon intermedius,* Coll. 1912. N. S.W." No collector or locality is given. This specimen had a sorus 5–7 cm. long and spores 7–12 μ diameter.

[14] Flore Francaise **6**: 76. 1815.
[15] Apercu Systematique des Ustilaginales 12. 1877.
[16] Ann. Sci. Nat. VI. **4**: 200. 1876.
[17] Ann. Sci. Nat. VI. **4**: 210. 1876.
[18] Oudemans, C. A. J. A. Enum. Syst. Fung. **1**: 704. 1919.
[19] Smuts of Australia 166. 1910.
[20] Ann. Myc. **26**: 32. 1928.
[21] Mycologia **22**: 139. 1930.

Yen,[22] in 1937, described and illustrated a smut on *Andropogon Lanigeri*, collected in Morocco, giving it the name of *Sphacelotheca columellifera* (Tul.) Yen, with spores 7.2–9.6 μ diameter.

From this brief review it is evident that there is confusion as to the identity of the Tulasne species referred to at the beginning of this paper. This is not surprising since the early writers listed so many unrelated hosts for *Ustilago Carbo*, its subspecies and varieties. The confusion cannot be wholly cleared up until many of the Tulasne specimens have been examined and named according to present day nomenclature.

Through the kindness of Dr. Roger Heim of the Museum National d'Histoire Naturelle, Laboratoire de Cryptogamie, Paris, France, two of the Tulasne specimens were loaned for examination. They are labeled as follows:

1. *Ustilago Carbo* γ *columellifera* a. *transfissa* Tul., on *Andropogon hirto*, LaCalle, Mai 1841.

2. *Ustilago Carbo* γ *columellifera* b. *trichophora* Tul., on *Cynodante Dactylon*, LaCalle, 13 July 1840.

The following descriptions are a result of a careful microscopic examination of these specimens.

1. USTILAGO CARBO γ COLUMELLIFERA a. TRANSFISSA Tul. Ann. Sci. Nat. III. **7**: 81. 1847.

Sori in the ovaries, 2–3 mm. long, concealed by the glumes, inconspicuous, ovoid, covered by a grey false membrane which flakes away revealing a dark agglutinated spore mass surrounding a columella; sterile cells hyaline, globose to subglobose, often irregular, usually in chains, variable in size, chiefly 7–10.5 μ diam.; spores globose to subglobose, sometimes irregular, dark-olivaceous to brown, subopaque, abundantly punctate, chiefly 10.5 to 14 μ diam.

On *Andropogon hirta*, LaCalle, Algeria, May 1841. Cryptogamie Ex. herb. Durieu de Maisonneuve. Legit L. Motelay (1878). Deposited in the Tulasne Herbarium, Museum National d'Histoire Naturelle, Laboratoire de Cryptogamie, Paris.

From the description we see that it is a *Sphacelotheca*, but that the spores are larger than those given by previous writers. The size of the spores do agree very closely to those given by Tulasne

[22] Rev. Myc. n.s. **2**: 76–78. 1937.

for *Ustilago Carbo* γ *columellifera,* viz. 9.6–12.8 μ diam. The writer, therefore, proposes the name **Sphacelotheca transfissa** (Tul.) Zundel, nom. nov. for this species (FIG. 3*A*).

FIG. 3. *A, Ustilago Carbo* γ *columellifera; a. transfissa* Tul.; *B, Ustilago Carbo* γ *columellifera; b. trichophora* Tul.

2. USTILAGO CARBO γ COLUMELLIFERA b. TRICHOPHORA Tul. Ann. Sci. Nat. III. **7**: 81. 1847.

Sori in the ovaries and inflorescence, 5–7 cm. long, cylindrical, covered with a grey membrane which flakes away revealing a granular, dark powdery spore mass intermixed with long shreds of host tissue; spore-balls dark, opaque, permanent, variously shaped, spheroidal to ellipsoidal, irregular, many spored 45–80 μ long; spores globose to subglobose, occasionally angled due to mutual pressure, light olivaceous brown, smooth, chiefly 3.5–6 μ diam., occasionally up to 7μ.

On *Paspalum distichum,* La Calla, Algeria, July 13, 1840. Cryptogamie Ex. herb. Durieu de Maisonneuve. L. Motelay (1878). Deposited in the Tulasne Herbarium, Museum National d'Histoire Naturelle, Laboratoire de Cryptogamie, Paris.

In order to be sure of the identity of this host, the specimen was sent to Mrs. Agnes Chase, of the U. S. Department of Agriculture, who reports that the host is not *Cynodon Dactylon* L. as labeled, but probably *Paspalum distichum* L.

The writer has not found a *Sorosporium* on *Paspalum* sp. that agrees with the one in question and therefore considers it undescribed.

An examination of this specimen was surprising in three ways: (1) The host is given as *Cynodon Dactylon* while in the original description Tulasne gives *Panicum Colonum* and *Pennisetum cenchroides* as the hosts, but later names other hosts including *Cynodon Dactylon*. (2) This smut is a *Sorosporium*. (3) The spores are smaller than those given by Tulasne for *Ustilago Carbo* γ *columellifera*. Apparently then this is an unnamed species and on that assumption the writer proposes the name **Sorosporium trichophorum** (Tul.) Zundel, nom. nov. (FIG. 3*B*).

It is now evident that the Australian specimen used by the writer in 1930 was mislabeled "*Cintractia columellifera*." It is an unnamed *Sphacelotheca* and the writer proposes the following:

Sphacelotheca MacAlpineae Zundel, sp. nov.

Sori destroying the inflorescence, long linear, 5–7 cm. long, at first concealed by the sheath but later protruding, covered by an evident yellowish white membrane which ruptures irregularly revealing a dark brown, agglutinated, spore mass surrounding a large well developed columella, false membrane breaking up into groups or chains of globose, hyaline, sterile cells, 7–12 μ diam.; spores chiefly globose, regular, light reddish brown, vacuolated under oil immersion, smooth, chiefly 7 μ diam., occasionally up to 9 μ.

Soris inflorescentiam destruentibus, longis linearibus, 5–7 cm. longis, primo in vagina celatis, postea protrudentibus, membrana lutescente tectis, quae irregulariter rupta massam atro-brunneam agglutinatam sporarum detegit magnam et maturam columellam circumcludentem, membrana falsa in glomerulas vel catenas cellarum globosarum, hyalinarum, sterilium rupente, 7–12 μ diam.; sporis plerumque globosis, regularibus, sub-rubro-brunneis, in "oleo" vacuolatis, levibus, plerumque 7 μ diam., raro usque ad 9 μ.

On *Andropogon intermedius* R. Br., New South Wales, Australia, Coll. 1912 (N. S. W. Dept. Agr., Biological Branch No. 8A, labeled *Cintractia columellifera*).

An examination of a specimen of *Ustilago columellifera* (Tul.) Yen and comparing it with the Tulasne specimen *Ustilago Carbo* γ *columellifera* a. *transfissa* shows that the two smuts are different. (1) The Yen specimen has smaller spores than the Tulasne specimen. (2) The Yen specimen has a larger sorus than the Tulasne

specimen. It, therefore, appears to be necessary to rename the Yen smut, and the writer proposes the following name, the description being practically identical to the original published by Yen:

Sphacelotheca Yenii Zundel, nom. nov.

Syn. *Sphacelotheca columellifera* Yen, Rev. Myc. n.s. **2**: 76. 1937.

Sori destroying the ovaries and inflorescence, 1–1.5 cm. long, covered by a grey false membrane which ruptures disclosing a powdery spore mass surrounding a thick columella; sterile cells abundant, globose to subglobose, singly or in chains, thick walled, hyaline, 10–21 μ diam.; spores globose to subglobose, reddish brown, smooth, chiefly 7–9 μ diam.

On *Andropogon Lanigeri* Desf., Skourat, Morocco, coll. G. Malençon.

VII. USTILAGINALES COLLECTED IN SOUTH EASTERN ASIA

This portion of the paper is to report collections of smuts from South Eastern Asia, which were sent to Dr. George P. Clinton for determination ten or more years ago. The writer found them when going through the Clinton collection of undetermined specimens after his sudden death.

Ustilago Cynodontis (Pass.) Curzi, on *Cynodon Dactylon* Pers., along road, Haiphong, Tonkin, Oct. 6, 1921, coll. A. S. Hitchcock (no. *19535*); in yard and along street, Vinh, Annam, Indo-China, Sept. 22, 1921, coll. A. S. Hitchcock (no. *19275*).

Sorosporium Arundinellae H. & P. Sydow, on *Arundinella Wallichii* Nees, Doniao South of Hanoi, Indo-China, Oct. 4, 1921, coll. A. S. Hitchcock (no. *19464*).

Sorosporium Chamaeraphis Sydow, on *Chamaeraphis muricata* (L.f.) Merr., Manila, Luzon, Philippine Islands, June 8, 1921, coll. A. S. Hitchcock (no number).

Sorosporium Cantonensis Zundel, sp. nov.

Sori destroying the inflorescence, long, linear, about 1 cm. long and 1 mm. wide, hidden by the glumes, the protruding end hardly visible, covered by a membrane which disintegrates into long

sterile cells which often adhere end to end forming hyphae like structures, revealing a granular spore mass surrounding a well developed columella; spore-balls subspheric to elliptic, opaque, many spored, usually disintegrating at maturity, 52–115 μ long; spores dark reddish-brown, opaque with a thick epispore, chiefly subspheric, irregular, often angular, smooth, chiefly 14–18 μ in length.

Soris inflorescentiam destruentibus, longis, linearibus, ca. 1 cm. longis et 1 mm. latis, in glumis fere celatis, membrana tegente in longas sterilesque cellas saepe hyphoide catenatas rumpente; massa sporarum granulata maturae columellae circumstante; glomerulis sporarum sub-sphericis vel ellipsoideis, opacis, sporis numerosis, plerumque mature dissolutis, 52–115 μ longis; sporis atrorubrobrunneis, opacis, episporiis crassis, plerumque subsphericis, irregularibus, saepe angularibus, levibus, plerumque 14–18 μ longis.

On *Cymbopogon hematatus,* Yinktak, on North river, 80 miles north of Canton, China. Coll. A. S. Hitchcock (no. *18822*), Sept. 9, 1921.

This species apparently is related to *Sorosporium geminellium* H. & P. Sydow & Butler, but differs in having a smaller and more slender sorus. The spores of both species are similar in size and shape but are entirely smooth in the species here described.

Sphacelotheca borealis (Clint.) Schell., on *Polygonum* sp., flats along river, 6 miles S.E. Harbin, Manchuria, June 17, 1925, coll. P. H. Dorsett (no. *3319*).

Sphacelotheca Hainanae Zundel, sp. nov.

Sori in the ovaries, elongated, about 2 mm. long, hidden by the glumes, at first covered by a light colored membrane which ruptures revealing a dark brown spore mass; sterile cells in groups, often cerebroid, yellowish, globose-angular, 7–12 μ diameter; spores globose to subglobose, regular, light reddish-brown, abundantly and finely echinulate, chiefly 8–10 μ long.

Soris in ovariis, elongatis, ca. 2 mm. longis, glumis celantibus, membrana albida, quae rupta massam atreo-brunneam sporarum detegit; cellis sterilibus et glomeratis, saepe cerebroideis, subflavis, globoso-angularibus, 7–12 μ diam.; sporis globosis vel subglobosis, regularibus, sub-rubro-brunneis, abundante et minute echinulatis, plerumque 8–10 μ longis.

On *Ischaemum rugosum* Salisb., Kachek, Island of Hainan, China. Coll. A. S. Hitchcock (no. *19610*), Oct. 13, 1921.

This species is closely related to *Ustilago tonglinensis* Tracy & Earle, but differs by the smaller, lighter colored spores and in being a *Sphacelotheca.*

VIII. NEW REPORTS OF NORTH AMERICAN USTILAGINALES

Cintractia caricis (Pers.) Magn. on *Carex aquatalis* Wahlb., swamp near Sooke Lake, Vancouver Island, B. C., Aug. 7, 1899, coll. M. A. Barber (no. *59*), from Farlow Herbarium, Harvard University; Kalispell Creek, Priest Lake, Bonner Co., Idaho, August 5, 1934, coll. J. H. Christ.

Ustilago chloridicola P. Henn. on ? *Chloris radiata* (L.) Swartz, Jamaica, British West Indies, Feb. 14, 1891, coll. R. Thaxter (acc. no. *78814*) from Farlow Herbarium, Harvard University.

Ustilago striaeformis (West.) Niessl, on *Poa trivialis* L., New Haven, Conn., 1887–1888, coll. R. Thaxter (acc. no. *7888*) from Farlow Herbarium, Harvard University; on *Phalaris arundinacea* L., Kitterary Point, Maine, coll. R. Thaxter (acc. no. *7892*), from Farlow Herbarium, Harvard University.

Ustilago utriculosa (Nees) Tul., on *Polygonum* sp., New Haven, Conn., 1887–1888, coll. R. Thaxter (acc. no. *7886*), from Farlow Herbarium, Harvard University.

Sphacelotheca Digitariae (Kuuze.) Clinton & Zundel, nom. nov., on *Digitaria horizontalis* Willd., near Kingston, Jamaica, British West Indies, 1891, coll. R. Thaxter (acc. no. *7885*), from Farlow Herbarium, Harvard University.

Tilletia oklahomae Zundel, sp. nov.

Sori in the ovaries, inconspicuous, concealed by the glumes, 3–4 mm. long, dark colored, sterile cells or immature spores rather abundant, hyaline, thick walled with granular contents, about the size of the spores; spores reddish-brown, regular, sphaerical to subspherical, densely covered with pointed spiney scales (about 2.5–3 μ), chiefly 17–21 μ in diam.

Soris in ovariis parum conspicuis, glumis celantibus, 3–4 mm. longis, fuscis, cellis sterilibus vel sporis immaturis aliquantum abundantibus, hyalinis, parietibus crassis, granulis internis, eadem ferme magnitudine qua sporis; sporis rubro-brunneis, regularibus, spheroideis vel subspheroideis, spinatis squamis (ca. 2.5–3 μ largis) dense copertis, plerumque 17–21 μ diam.

On *Aristida longespica* Poir., Tulsa, Oklahoma, coll. Mrs. Harriet Barclay, Nov. 1937, comm. W. W. Diehl.

Urocystis occulta (Wallr.) Rab., on Scale cereale L., New Haven, Conn., 1887–1888, coll. R. Thaxter (acc. no. *7887*), from Farlow Herbarium, Harvard University.

IX. NEW SPECIES FROM VARIOUS PARTS OF THE WORLD

Sphacelotheca Botriochloae Zundel, sp. nov.

Sori in the inflorescence, destroying it, long linear, 4–6 cm. long, covered with a dark brown to reddish false membrane which ruptures revealing a dark reddish brown, powdery, spore mass surrounding a well developed, simple columella; sterile cells chiefly globose to somewhat angled by compression, single or in groups, tinted brown, 10–14 μ diam.; spores chiefly globose to ellipsoidal, sometimes angled, reddish-brown with a thick darker colored epispore, minutely echinulate, 7–8 μ in diam.

Soris inflorescentiam destruentibus, longis, linearibus, 4–6 cm. longis, membrana falsa atro-brunnea vel rufa, quae rupta massam atro-rubro-brunneam atque pulverulentam sporarum, maturam simplicemque columellam circumcludentem, detegit; cellis sterilibus, plerumque globosis vel aliquantulum per compressionem angularibus, singularibus vel glomeratis, brunneis, 10–14 μ diam.; sporis plerumque globosis vel ellipsoideis, interdum angularibus, rubro-brunneis, episporo crasso et atriore minute echinulatis, 7–8 μ diam.

On *Botriochloa decipiens,* Walla Walla, New South Wales, Australia, coll. R. A. Black, May 17, 1937.

Sphacelotheca nankinensis Zundel, sp. nov.

Sori destroying the inflorescence, long, linear, chiefly 8–10 cm. long, mostly concealed by the sheaths, covered by a dark brown membrane which flakes away revealing a dark brown, dusty spore mass surrounding a long columella; sterile cells abundant and in groups, tinted light yellow, variable in size, 24–70 μ long, spores spheric to subspheric, regular, light reddish-brown, smooth, chiefly 4–6 μ long.

Soris inflorescentiam destruentibus, longis, linearibus, plerumque 8–10 cm. longis, plerumque in vaginis celatis, atro-brunnea membrana tectis; membrana rupta atro-brunneam sporarum massam longae columellae circumstantem detegit; cellis sterilibus glomerulatim abundantibus; sub-flavidis; in magnitudine variabilibus, 24–70 μ longis, sporis sphericis vel sub-sphericis, dilute rubro-brunneis, levibus, plerumque 4–6 μ longis.

On *Imperata arundinacea* Cyrilli, Kee-ling Sze, Nanking, prov. Kiangsu, China, coll. by G. N. Stewart, com. by R. H. Porter (no. 265).

This smut differs from *Sphacelotheca Schweinfurthiana* (Thüm.) Sacc. by the smaller, lighter colored spores and by the large groups of sterile cells which are very characteristic. The sterile cells are usually in sub-spheric groups which give a cerebral

appearance, or sometimes they are in long chains having the appearance in general of a braided rope.

Sphacelotheca Papuae Zundel, sp. nov.

Sori destroying the ovaries, 2 mm. long, protected by the glumes, at first protected by a delicate membrane, columella well developed; sterile cells usually in groups, globose or frequently collapsed, often irregular, hyaline, thin-walled, 14–18 μ diam.; spores reddish-brown, globose or slightly subglobose, regular, minutely but abundantly verruculose, chiefly 9–10 μ diam.

Soris ovaria destruentibus, 2 mm. longis, glumis protegentibus, primo membrana delicata tectis, columella bene aucta, cellis sterilibus, plerumque in glomerulis, globosis vel frequenter collapsis, saepe irregularibus, hyalinis, parietibus tenuibus, 14–18 μ diam.; sporis rubro-brunneis, globosis vel leviter subglobosis, regularibus, minute sed abundanter verruculosis, plerumque 9–10 μ diam.

On *Saccharum arundinacea* Retz., on Fly River, 30 miles below Everill Junction, Papua (British New Guinea), coll. Brass (no. *6582*, Archbold Expedition), May 1936.

This species is closely related to *Sphacelotheca Schweinfurthiana* (Thüm.) Sacc., but differs in having verruculate spores while the spores of *S. Schweinfurthiana* are smooth.

Sphacelotheca Viegasiana Zundel, sp. nov.

Sori destroying the inflorescence, partially concealed by the sheath; 2–5 cm. long, covered by a brown membrane which disintegrates revealing a dark brown, powdery spore mass surrounding a thick columella, sterile cells of false membrane at first in chanes but later disintegrating into pairs or singly, subglobose to ellipsoidal, hyaline, 7–14 μ long; spores globose to subglobose, regular, olivaceous-brown, smooth, chiefly 7–8 μ in diam.

Soris inflorescentiam destruentibus, partim vagina celatis, 2–5 cm. longis, membrana brunnea, massa sporarum atro-brunnea pulverulenta, columella crassa, cellis membranae falsae sterilibus primo in catenas, deinde binatim vel singulatim disintegratibus, subglobosis vel ellipsoideis, hyalinis, 7–14 μ longis; sporis globosis vel subglobosis, regularibus, olivaceo-brunneis, levibus, plerumque 7–8 μ diam.

On *Trichachne saccariflora* (Raddi) Nees, Terreno baldio, Campinas. Est. S. Paulo, Brazil, coll. A. P. Viegas, Oct. 5, 1935 (no. *2554*).

Sorosporium Yoshinagae Zundel, sp. nov.

Sori destroying the inflorescence, long, linear, 6–9 cm. long, at first concealed by the sheaths and covered with a delicate membrane which flakes away revealing long shreds and a dark brown spore mass which soon becomes powdery; spore-balls rather evanescent, regular, ovate, opaque, dark brown with numerous spores, chiefly 70–105 μ long; spores reddish-brown, spheric to subspheric, smooth, chiefly 4–6 μ in length.

Soris inflorescentiam destruentibus, longis linearibus, 6–9 cm. longis, primo membrana delicata in vagina tectis, quae membrana rupta fibrillas longas et massam atro-brunneam mox pulverulentam sporarum detegit; glomerulis sporarum aliquantulum evanescentibus, regularibus, ovatis, opacis, atro-brunneis, sporas numerosas habentibus, 70–105 μ longis; sporis atro-brunneis, spheroideis vel sub-spheroideis, levibus, plerumque 4–6 μ longis.

On *Panicum repens* L., Trino-mura, Tosa, Japan. Coll. by T. Yoshinaga, Aug. 8, 1922.

Cintractia nova-guineae Zundel, sp. nov.

Sori in the ovaries, rather completely hidden by the glumes, oblong to subspherical, 3–5 mm. long, somewhat agglutinated to powdery; spores globose to subglobose or sometimes subcircular by mutual compression, intermixed with reddish-brown, collapsed host cells, dark reddish-brown, usually with remains of enveloping membrane showing as hyaline to brown lateral wings, minutely pitted, 17.5–21 μ diam.

Soris in ovariis, glumis paene omnino celatis, oblongis vel subspheroideis, 3–5 mm., aliquantum agglutinatis vel pulverulentis; sporis globosis vel subglobosis, interdum per compressionem inter se subcircularibus, rubro-brunneo colore intermixtis, cellis hospitis collapsis, atro-rubro-brunneis, plerumque partibus membranae restantibus, velut hyalinis vel brunneis lateralibus alis apparentibus, minute porosis, 17.5–21 μ diam.

On *Rhynchospora aff. glauca,* Marsh Meadows, Morobe, New Guinea, coll. Mrs. Clemens, Dec. 22, 1938. Comm. Dr. George B. Cummins.

This smut is closely related to *Cintractia amazonica* Sydow, but differs by having a larger sorus and by having the spores minutely pitted while the spores of *C. amazonica* are verruculate. Some *Juncus* sp. was mixed in the collection.

PENNSYLVANIA STATE COLLEGE

HOST INVASION IN SYSTEMIC INFECTIONS OF UROMYCES CALADII

S. M. Pady *

(with 3 figures)

Uromyces Caladii is a systemic perennial rust on *Arisaema triphyllum*, the well known and widely distributed Jack-in-the-pulpit, and on *A. Dracontium*, Dragon Root. Leaves and flower parts show evident infection as they unfold in the spring with pycnia covering the lower surface of the leaves, the spathe and often the spadix as well, followed later by the aecia. In this autoecious rust the uredinia are formed during the summer in localized infections, followed by the telia which either replace the uredinial pustules, or form in separate sori.

For some time the writer has been interested in some of the rusts which are systemic and perennial: *Hyalopsora aspidiotus*, whose diploid mycelium systemically infects the fern, *Phegopteris* (**6**); *Calyptospora Geoppertiana*, whose haploid systemic mycelium causes Witches Brooms on blueberries (**5**); *Gymnoconia interstitialis*, the well known Orange-rust of wild and cultivated blackberries (**7**). This paper presents the results of observations made in connection with the study of the distribution of the mycelium of *Uromyces Caladii* in the dormant and the growing tissues of *A. triphyllum*.

Freehand and prepared sections through dormant infected corms reveal the presence of mycelium in practically all of the tissues. The lower half of the corm, which is relatively free from starch, contains a much greater amount of mycelium than the upper starch-filled region. The mycelium is typically intercellular with moderately broad uninucleate hyphal cells filled with dense cytoplasm. In certain regions the mycelium is especially abundant and the host

* The writer takes this opportunity of thanking Dr. G. W. Keitt, Head of the Department of Plant Pathology, University of Wisconsin, and other members of the staff, for courtesies generously extended during the summer of 1937.

cells may be almost completely surrounded by hyphae, with numerous slender coiled haustoria projecting into adjacent cells. These areas usually involve about a half a dozen or more of the large parenchymatous cells and are found only in the lower half of the corm. In many cases the mycelium evidences a preference for the vascular bundles, often being found in close association with the vascular elements. The upper part of the corm consists of a large smooth conical bud made up of a median growing point completely enclosed by two rudimentary leaves, one inside the other, and four outer fleshy bracts. If the corm is large enough to produce flowers a rudimentary flowering stalk will be formed immediately above the growing point. All of these structures may contain mycelium. Large corms may bear one or more offsets on the upper margin and these also have been shown to possess mycelium in all tissues.

When growth begins in the spring the mycelium keeps pace with the growing tissues as indicated by the presence of hyphae in the above-ground parts. Three of the bracts remain rudimentary while the fourth grows large enough to protect the leaf as it pushes through the soil, remaining at the base as a membraneous sheath (**8**). Invasion of this bract is evidenced by the later appearance of pycnia and sometimes aecia. At this time long white fleshy roots, often terminating in offsets, arise from the upper surface of the corm penetrating the soil for a considerable distance. Preliminary examination of these roots failed to reveal any trace of mycelium. A careful study of prepared slides made from similar roots has confirmed this observation. If the mycelium invades the root at all it must be when the root is beginning to form, because older roots are certainly free from the rust. In this case, the host tissues have outgrown the fungus. There is also the possibility that the mycelium does not invade even the youngest roots.

MYCELIUM IN THE PETIOLE OF THE LEAF

The mature leaf of *Arisaema triphyllum* is a large tri-radiate structure with a stout petiole, which may reach a height of 24″ or more. The petiole consists of an outer epidermis followed by several layers of fairly compact parenchymatous cells. From this point, progressing toward the center are found many large air spaces which give the central part of the stalk a spongy appearance.

This spongy parenchyma is characteristic and is "of a special and peculiar form, in which the cells are arranged to make a series of fluted columns" (1). The large air spaces formed by these columns constitute an ideal growing region and mycelium is very abundant here. Occasionally, the fungus invades the scattered bundles; but more often is found in the parenchyma immediately surrounding the bundle. Another favorite region is in the intercellular spaces of the cells which lie just beneath the epidermis. The amount of mycelium present in a petiole is extremely variable, ranging from a condition where the distribution is relatively uniform to one where the hyphae occur only in a few isolated patches.

MYCELIUM IN THE LEAF BLADE

Lesions of various sizes characterize the upper surface of infected leaves. These lesions vary from pale yellowish-green to whitish in color, and form a striking contrast to the disease-free tissues (FIG. 1). It has been found that these areas represent very accurately the extent of mycelial invasion and that the mycelium is confined to these areas. The precise limits of the infected tissues may be readily determined, as well as the percentage of infection. While only a few percentages have been accurately worked out, it is possible to arrange infected leaves in a graded series which would demonstrate all degrees of infection from a trace to one hundred percent. Sometimes one leaflet alone will be infected, while the other 2 leaflets are free. In most cases, however, where one leaflet shows infection the others also will show it (FIG. 1). Where the percentage of infection is low the infected areas are invariably confined to the regions immediately bordering the mid-rib of the leaflet, and usually extend the entire length of the blade. These areas are extremely irregular and often extend out into the adjacent mesophyll as whitish projections of varying lengths and widths. The leaf shown in figure 1 demonstrates this very clearly, the lesions being confined to the mid-rib region and extending to the tip of each leaflet, while in 3 places the lesions extend all the way to the margin.

In order to estimate the percentage of infection in the leaf shown in figure 1, the outline of the leaf was traced on squared graph paper. The infected areas were very carefully outlined by the same

method. The total area of all 3 leaflets was found to be 7800 sq. mm.; the total infected area was 2112 sq. mm.; the percentage of infection was 27.0 per cent. The individual leaflets had the following percentages: Leaflet 1 (on the right) 16.8 per cent, Leaflet 2 (top) 46.7 per cent, Leaflet 3 (at left) 31.3 per cent.

The photograph in figure 1 also shows clearly another effect upon leaf tissues, namely that of distortion. The presence of mycelium retards the normal ontogeny of leaf tissues and the infected areas are generally much smaller and as a result the leaf is usually very

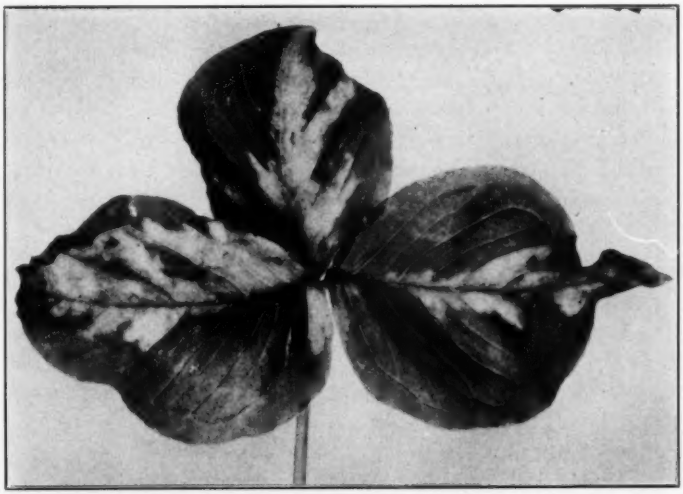

FIG. 1. Leaf of *Arisaema triphyllum* infected with *Uromyces Caladii*.

irregular in outline. This stunting effect becomes clear when the infected areas are compared with the disease-free tissues. For example, the lower halves of the 2 basal leaflets in figure 1, which are practically disease free, are appreciably larger than adjacent infected areas. This is even more clearly shown where one or two leaflets are heavily infected, while the remaining leaflets are relatively free. In such cases the diseased leaf is not only distorted but is greatly reduced in size. This is shown by the following figures obtained from a partially infected leaf. Leaflet 1 was free from the rust and had a total area of 5036 sq. mm.; Leaflet 2 with

54.8 per cent infection had an area of 3372 sq. mm.; Leaflet 3 with 53.4 per cent infection had an area of 3500 sq. mm. The disease free leaflet thus had an increased surface area of between 1664–1738 sq. mm. Leaves with a high percentage of infection are greatly reduced in size and shape, the latter changing from the normal lanceolate to an irregular oval or round, and the tip from long acuminate to mucronate.

The mycelium in the leaf tissue is confined largely to the spongy parenchyma, although both epidermis and chlorenchyma are infected. In leaves which are partially infected the mycelium is often delimited by the large veins which run out pinnately from the midrib. These large veins appear to be an effective boundary (FIG. 1, left leaflet). Pycnia are formed on the lower surface in the substomatal air chambers and in their vicinity the mycelium is particularly abundant, as Rice has pointed out (**9**). Aecia are formed in the spongy parenchyma and in the neighborhood of the aecial primordia the mycelium is also abundant.

MYCELIUM IN THE FLOWER

The flower bud arises inside the two leaf primordia and grows out through the petiole a short distance above the axil of the 2 leaves about the same time as the leaves are unfolding. The mycelium which was in the growing point has grown rapidly in the young flower stalk keeping pace with the host tissues. The spongy nature of the stalk and of the spathe and spadix provides ideal conditions for rapid mycelial growth. Freehand and prepared sections of both the stalk and spadix reveal abundant mycelium in the large open spaces between the columns. Almost immediately pycnia may be observed on the spathe and on the flower stalk; later, these will be followed by aecia.

The spadix consists of a central axis made up of the spongy parenchyma mentioned earlier, terminated by a large sterile club-shaped structure usually purple in color and subtended by the stamens and ovaries. *Arisaema* is usually dioecious with the staminate and pistillate flowers on separate plants. In both cases the flowers are in a cluster at the base of the spadix, usually separated from the upper sterile portion by a narrow neck. The filaments are short and bear the anthers at the tip, these having four

small locules. Mycelium is present in the filament and in the portion of the anther lying between the locules, but none has ever been found in the tapetum, spores or locules. Occasionally pycnia are present on the sterile club and they have been found also on the filaments of the stamens.

The ovulate flowers consist of single unilocular gynaecia, clustered about the base of the spadix. In each ovary 5 orthotropus ovules are formed arising from the placenta. The tip of the ovary is somewhat conical and is surmounted by a stigma consisting of elongated unicellular cells resembling young root hairs. Figure 2*A* is a section of a young flower in the megaspore mother cell

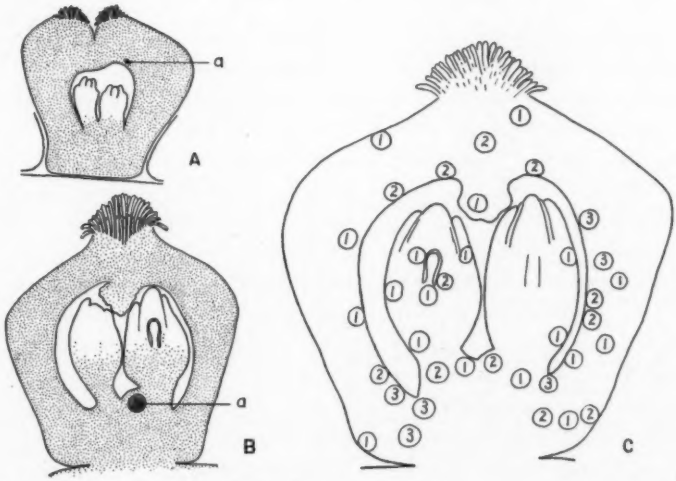

FIG. 2. *Uromyces Caladii.*

stage, with young stigma, stylar canal and 2 ovules each with a megaspore mother cell, nucellus and an outer and inner integument. Figure 3*A* is a photomicrograph of an ovulate flower of the same age.

The distribution of the mycelium in the young ovary is shown diagrammatically in Figure 2*A* by the stippled areas. All tissues except those of the ovule contain fungus hyphae. While some variation exists, the mycelium at this stage has reached a point midway up the funiculus. This shows very clearly in the slide

from which figure 3*A* was taken; in the photograph, however, the mycelium cannot be clearly seen. Evidently the ovules grow very rapidly and for a time at least outstrip the fungus, although the mycelium actually does invade the ovule later. In ovaries of this stage, that is, the megaspore mother cell stage, pycnia may begin to form and the tiny rudiments may often be found, as for example in figure 2*A*, *a*. Such cases are indeed rare and have been observed only 3 times, twice in the ovule wall (FIG. 2*A*, *a*), and once in the centre of the ovule at a point much higher than the line indicated in figure 2*A*.

INTERNAL PYCNIA IN OLDER OVULES

During the summer of 1937 a number of infected plants were grown in the greenhouse, of which there were several staminate and pistillate plants. The particular plant which furnished the material for the study of older ovules was one of 2 remaining pistillate plants. Artificial pollenation was employed in order to ensure fertilization, the pollen being transferred by means of a camel's hair brush. Eight days later the material was fixed and studied. From the condition of the embryo (FIG. 3*B*, *D*) it is evident that the pollenation was successful, although it is difficult to determine whether it was due to natural or to artificial pollenation.

A comparison of figures 2*A* and 2*B* or of the photographs 3*A* and 3*B* shows clearly the tremendous increase in size of all parts of the ovary and especially of the ovule. The mycelium has grown up into the developing ovule reaching the nucellus and integuments (FIG. 2*B*). No instance of mycelium in the tip of the ovule has ever been observed. The fungus threads are well filled with cytoplasm and appear to be growing rapidly. Mature and developing pycnia are abundant (FIG. 3*B*, *C*, *D*, *E*). The number of pycnia per ovulate flower averages 5–8; in the flower shown in section, in figure 3*B*, three other pycnia were present, making a total of five. Except for the smaller size and the loss of paraphyses these pycnia appeared quite normal. Spermatiophores line the cavity projecting toward the centre (FIG. 2*B*, 3*D*, *E*). Occasionally spermatia were exuded into the surrounding tissues (FIG. 3*B*). Where the pycnia opened into the locule, some paraphyses

were present and spermatia occurred in abundance. The latter appeared quite normal, at least insofar as staining was concerned.

Figure 2*C* is a diagrammatic summary of the number and distribution of these pycnia. All of the pycnia found in 12 ovaries were counted and their position was marked by a circle; the number appearing in that region was designated by a figure inside the circle. An analysis of figure 2*C* is found in Table I.

TABLE I

ANALYSIS OF FIGURE 2*C*

Total number pycnia checked	59
Deep seated abnormal	41
Pycnia near edge (FIG. 3*B*) but never opening to outside	9
Pycnia projecting into locule	14
Pycnia opening to outside	4
Pycnia in ovule (FIG. 3*F*)	7 (11%)
Pycnia in funiculus (FIG. 3*C, D, E*)	3 (5%)
Pycnia in placenta (FIG. 2*B*, 3*B*)	12 (20%)
Pycnia in ovary wall (FIG. 3*C*)	37 (64%)

Another explanation of the rapid invasion of the ovule by the mycelium is by lateral infection from the ovary wall instead of basal infection through the funiculus. In many cases (FIG. 3*A, E, F*) the ovule is very close to the ovary wall. Where actual contact occurred it would be relatively easy for the mycelium to enter the integument. Some of the ovaries of the material used in working out figure 2*C* were sectioned transversely and revealed 5 rather crowded ovules. In one case a young pycnial fundament was present in the integument at the nearest point to the ovary wall. Running from the fundament were several strands of mycelium which could be clearly traced to the ovary wall. This explanation might also account for the pycnium found in the very young ovule referred to earlier.

The presence of small pycnia in the ovule (FIG. 3*F*) proves that the mycelium invades this tissue very rapidly and soon forms fruiting bodies. The important question here is whether the young embryo contains mycelium or not. A study of many sections failed to reveal any signs of hyphae. Since the embryo has arisen from the fertilized egg cell and has grown very quickly it would become infected only when mycelium was present in the embryo sac or in great abundance in the nucellus. The chances

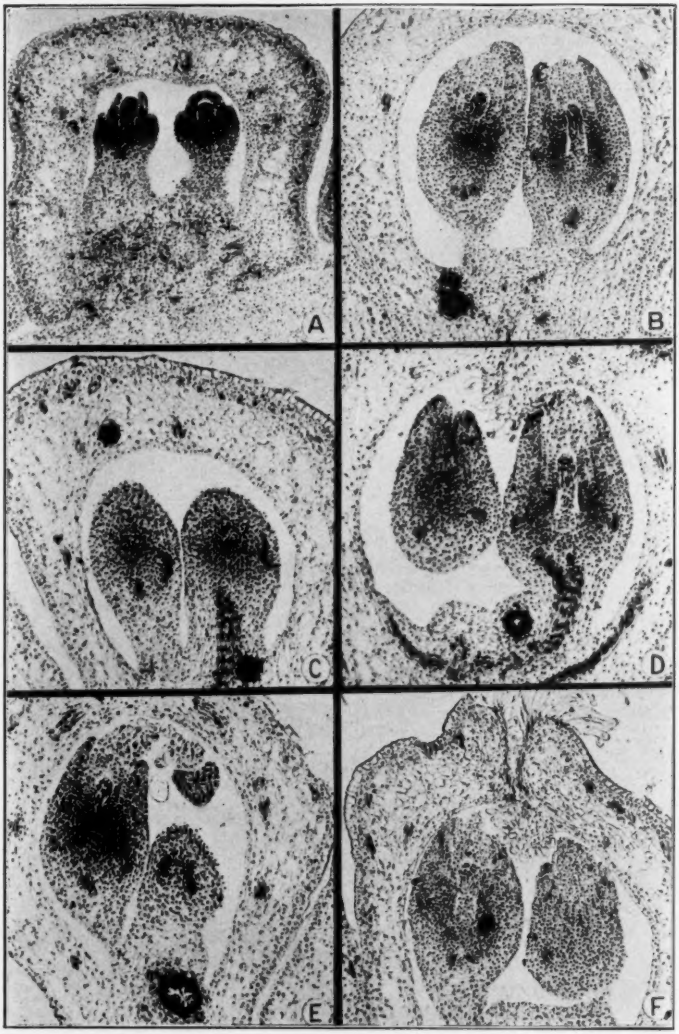

FIG. 3. Infection in *Uromyces Caladii*.

of the very young embryo becoming infected are thus very slight, although the surrounding tissues may be heavily infected. It would require a very rapidly growing mycelium to invade the young embryo.

Nine pycnia have been found in the older ovule (FIG. 2*C*) of which 4 were deeply seated in the tissues immediately surrounding the nucellus (FIG. 3*F*). One occupied a position in the nucellus about the level of the tip of the embryo; 2 were situated in the tissues opposite the base of the embryo; while the 4th lay immediately below the basal part of the embryo. In 3 of these the pycnium projected slightly into the space between the nucellus and the embryo.

MYCELIUM IN THE SEED

Considerable time and effort have been spent in studying seeds for the presence of the fungus, but results to date have been inconclusive. It should be borne in mind that systemically infected plants rarely flower and produce seed (**4**). This is partly true of *Arisaema* but there are several cases where systemically infected plants have produced seeds. The writer is of the opinion that the seeds may and do transmit the disease. This belief is based on the fact that the mycelium invades the young ovules and is present at the base of the young embryo. Further evidence was found in one plant, no. 48, which produced flowers in the greenhouse. This plant was pollenated to ensure fertilization. Twenty-two days later the fruit was harvested and young seeds showed unmistakable signs of infection.

Conclusive proof necessitates finding mycelium in mature seeds in plants grown under natural conditions. Numerous collections of seeds have failed so far to reveal any signs of mycelium. This problem will be further studied during the coming growing season.

OBSERVATION ON GROWTH OF DISEASED CORMS

It was decided to study the behavior of infected plants over a period of a number of years.[1] Large numbers of plants were gathered in the spring of 1936 and potted. During the summer of 1937 these corms were grown in the greenhouse of the Depart-

[1] Problem suggested by Professor H. S. Jackson, University of Toronto.

ment of Plant Pathology, University of Wisconsin. Corms were planted in individual pots on June 5th, 1937, and careful observations were made on the time required (1) for pycnia to appear, (2) for aecia to be formed. *Arisaema triphyllum* is a cool weather shade plant and great difficulty was encountered in keeping the plants growing, due to the high temperatures and other unfavorable conditions in the greenhouse. Many of the corms failed to germinate and the mortality among those that did grow was very high. The following table summarizes the observations made on the remaining plants:

TABLE II

LENGTH OF TIME REQUIRED FOR PYCNIAL AND AECIAL STAGES TO APPEAR WHEN GROWN UNDER GREENHOUSE CONDITIONS

No. of days after planting	16	19	23	26	30	33	37	40	44	47
Plants showing pycnia	21	55	45	42	35	37	33	31	28	27
Plants showing pycnia and aecial fundaments	0	3	20	26	32	30	31	32	31	29
Plants showing pycnia and aecial sori	0	1	1	2	5	7	6	5	5	4
Total infected plants	21	59	66	70	72	74	70	69	64	60
Total plants dead or dying or failed to grow	—	—	—	—	—	28	32	33	37	42

At the end of 16 days 21 plants showed aecia. By the 19th day 55 plants showed aecia, 3 additional plants showed aecial fundaments and 1 plant had a few aecia. On the 23rd day 45 plants were in the pycnial stage and 20 had developed aecial fundaments. From this time on there was a gradual increase in the number of plants showing aecia, and aecial fundaments. Pycnia continued to appear up to about the 33rd day. Many plants remained in the pycnial stage for the entire period. Many others developed fundaments, but failed to produce sori. The mortality is indicated by the figures in the 6th row.

DISCUSSION

Systemic infections imply invasion of all tissues in certain parts of a plant. Theoretically it is possible for a plant to become so completely parasitized that no part is free from the fungus. Actually such cases are extremely rare, even in the systemic rusts which are perennial. Arthur (2) uses the term "systemic" to apply to invasions of a portion of the plant. In *Melampsorella elatina* the fungus is confined to the tips of certain branches giving a witches

broom effect and causing the new leaves and shoots produced each spring to be infected. Here the infection is clearly systemic but only a part of the host is involved.

Uromyces Caladii is unusual in that the entire plant, with the exception of the roots, may be systemically infected. The effects of such infection are found in the tendency to suppress sexual reproduction, distortion of the leaves, and in the shortening of the growing period. Rapidly growing tissues may outgrow the fungus. In *Arisaema* the roots of infected plants are regularly free from the rust, and this in all probability is due to very rapid growth early in the season when conditions are favorable. In blackberries systemically infected with *Caeoma nitens,* sporulation begins early in the growing season and ordinarily all leaves are heavily rusted. The writer has observed that new leaves forming at the tip of the shoot, at the time the fungus is beginning to sporulate, are usually free from the rust. Part of the explanation doubtless lies in the fact that the host tissues have simply outgrown the fungus, since the leaves are devoid of hyphae; part of the explanation seems to involve the following fundamental principle. Two definite phases of growth are distinguishable in this systemic perennial mycelium. The first phase is that of *vegetative growth* and the establishment of the mycelium in the host. This takes place while the host tissues are developing at the beginning of the growing season. As the host tissues mature the fungus begins the second phase, namely *reproduction,* and sporulation commences. The onset of the second phase marks the end of the vegetative growth, and subsequently the mycelium does not invade new host territory. In *U. Caladii* disease free portions of the leaf will not be invaded after pycnia and aecia appear. In *C. nitens,* leaves formed during the first phase would be rusted but leaves formed during the second phase while sporulation was taking place would be free from the rust.

The percentage of infection is the measure of success achieved by the rust during the first phase of growth. One factor which would aid materially is the amount of mycelium originally present in the leaf primordium. Abundant hyphae would tend to result in a high percentage of infection. Sections through petioles show a great variation in the amount of mycelium; heavily infected leaves have plenty of mycelium; lightly infected leaves show only

occasional strands. The amount of mycelium therefore in the leaf would be dependent upon the amount of mycelium in the leaf primordium. There is evidently a very definite correlation between the percentage of infection and the amount of mycelium in the dormant corm. Numerous factors would influence the relative abundance of mycelium; the amount of growth made by the host the previous year; the amount of growth made by the fungus; the number of years infected; the age of the corm when primary infection occurred. The susceptible period is certainly very short since it is a common sight to see one heavily infected plant completely surrounded by healthy individuals. From such a plant there would be sufficient inoculum to infect every healthy plant in that immediate vicinity. In order to become systemic the mycelium must become established in the growing point of the corm. It has been shown by Dodge (**4**) and also by Pady (**7**) that the susceptible period for blackberries is just as the shoot pushes through the ground. If basidiospores of *C. nitens* fall on the shoot at this time the mycelium will invade the crown and in the following spring will be found in the growing points. One reason for the ease with which blackberries are infected is that the crown is very close to the ground level and the distance the mycelium will have to travel during that first year is very short. Arber (**2**) and Rennert (**8**) have shown that the corms of *Arisaema* tend to become deep seated as the result of the action of the contractile roots. Basidiospores falling on the shoot at the ground level would have to invade the corm, several inches away, before the above ground parts die off. Doubtless many plants become infected with basidiospores, but the majority will likely remain as local infections dying off at the end of the growing season. The growing season for *Arisaema* is very short and this would tend to make infection even more difficult. Part, if not all, of the explanation for the paucity of primary infections lies in the fact that the corms normally do not remain near the surface of the ground.

Arthur's (**2**) theory that the orientation of sori is controlled by nearness to the surrounding atmosphere, due to diffusion of air through stomata or epidermis, is probably correct. Normal pycnia of *U. Caladii* are substomatal and may be explained on this basis. In explaining the change of orientation of deep seated sori Arthur

postulated the presence of nearby cavities or locules in the tissues which cause the sori to grow toward them. The internal pycnia described by Stampfli (**10**) for *U. pisi* are all projecting into the locules of the flower. In *U. Caladii* however, there are more deep seated pycnia than there are those which open to the locules or to the atmosphere. Obviously, Arthur's explanation does not hold for *U. Caladii*. The theory that internal sori follow the line of least resistance (**3**) (**11**) does not apply to this particular rust since about 36 per cent of the pycnia lie in the compact tissues of the placenta, funiculus and ovule. The high percentage of internal pycnia in the ovary wall (64 per cent) is probably due to the fact that this tissue is the older and the hyphae had an excellent opportunity of becoming established there. The next oldest tissues are those of the placenta region (**2**) and the number of pycnia is correspondingly greater than in the relatively young tissues of the ovule.

It is surprising that there are so few pycnia on the outer surface of the ovary, since this tissue was not expanding any more rapidly than the tissues which contain the internal pycnia. Many of the pycnia lie so close to the surface that it would be relatively easy for them to force apart the overlying tissues. The upper pycnium in figure 3*B* lies but one cell below the cavity of the locule. Most of the pycnia appear to be functioning, as witnessed by the production of spermatia which are often extruded into the tissues. Modifications of these internal sori lie first in the suppression of the paraphyses and secondly in the occasional reduction of size. The comparison of figures 3*E* and 3*F* indicates that often the internal sori reach a considerable size, as large in fact as typical sori of the leaf. All such internal sori are atypical and probably should be regarded "as teratological phenomena of no special morphological significance" (**3**).

The questions of heterothallism, fertilization and diplodization are still under investigation. The failure of the plants grown in the greenhouse to produce aecia (Table II) may have been due to the unfavorable growing conditions since many plants remained in the pycnial stage. To all outward appearances, however, conditions were favorable, the pycnial nectar was abundant, insects were present and in the mornings the temperature was low and

humidity fairly high. Is it not possible that failure to produce aecia is due to the presence in separate plants of heterothallic races? Monosporidial infections undoubtedly take place in nature. On the other hand, if the perennial mycelium was made up of mixed races, how would fertilization occur? Would diplodization take place through mycelial fusions within the tissues or would there need to be a mixing of nectar from the different kinds of pycnia? In nature many "sterile" plants have already been found and others with but a few aecial sori surrounded by old and dying pycnia. The explanation of these two phenomena is purely a matter of conjecture. *Uromyces Caladii* seems to be favorable material for further investigations along these lines.

SUMMARY

Dormant corms of *Arisaema triphyllum* are systemically infected with the haploid mycelium of *Uromyces Caladii*. When growth begins in the spring, leaves and flowers become infected but roots remain free. In the leaf, mycelium is revealed by lesions on the upper surface, from which the percentage of infection may be estimated. The percentage varies from a trace to 100 per cent. In the flower mycelium invades all tissues of the spathe and spadix. Internal pycnia are found in the ovulate flowers, usually 5–8 per ovary and located in the ovary wall (64 per cent), placenta (20 per cent), funiculus (5 per cent), ovule (11 per cent). The mycelium invades the ovule and the young embryo suggesting the possibility of transmission of the disease through the seed.

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EXPLANATION OF FIGURES

Fig. 1. Leaf of *Arisaema triphyllum* infected with *Uromyces Caladii*. Total leaf area 7400 sq. mm. Infected area 2112 sq. mm. (28.5 per cent). Photograph by Eugene Herrling.

Fig. 2*A*. Longitudinal section of young ovary showing two ovules at the megaspore mother cell stage. Stippled area represents the presence of mycelium. Young pycnium shown at *a*. Compare with figure 3*A*. Camera lucida outline drawing. Fig. 2*B*. Longitudinal section through ovary 8 days after pollenation. Note the developing embryo, internal pycnium at *a*, the invasion of the ovule by mycelium. Compare with figure 3*D*. Camera lucida outline drawing. Fig. 2*C*. Diagram of an ovary to show the location of the internal pycnia in the flower. Pycnia are represented by circles and the number inside the circle indicates the number of pycnia found in that region. Of the 59 pycnia shown, 41 are deep seated. Average number of pycnia per ovary is 5–8.

Fig. 3*A*. Photomicrograph of young infected ovary. Compare with figure 2*A*. Fig. 3*B, C, D, E*. Photomicrographs showing internal pycnia in various tissues of the flower. Fixative made 8 days after pollenation. Fig. 3*F*. Young pycnium in nucellus of ovule. (Photomicrographs by Eugene Herrling.)

STERILE CONKS OF POLYPORUS GLOMERATUS AND ASSOCIATED CANKERS ON BEECH AND RED MAPLE

W. A. Campbell and Ross W. Davidson

(with 2 figures)

INTRODUCTION

In 1930 Hirt [1] reported sterile conks on beech (*Fagus grandifolia* Ehrhart.), which were associated with a normal fruiting body of *Fomes Everhartii* (Ellis & Gall.) Schrenk. During the summer of 1938 another type of sterile conk, with or without associated cankers, was found commonly on beech in the Green Mountain National Forest. These sterile conks, except for their smaller size, resembled those on birch recently reported by Campbell and Davidson [2] to be a sterile form of a *Poria* (probably *Poria obliqua*). Because of this resemblance and because *P. obliqua* or a similar *Poria* had been collected on beech in Pennsylvania and New Hampshire, it was originally thought that the sterile conks might be the sterile form of it. However, pure cultures of *Polyporus glomeratus* Peck, described by the writers,[3] were isolated from the sterile conks and the associated decay. In addition, *P. glomeratus* fruited on down beech on which there were sterile conks and cankers.

Later in the season a number of red maples (*Acer rubrum* Linn.) on the Gale River Experimental Forest, New Hampshire, were found to be badly cankered and decayed. Sterile fungus material characteristic of *P. glomeratus* was associated with the cankers and pure cultures from this material and from the decay confirmed the

[1] Hirt, Ray R. *Fomes Everhartii* associated with the production of sterile rimose bodies on *Fagus grandifolia*. Mycologia **22**: 310–312. 1930.

[2] Campbell, W. A. & Ross W. Davidson. A *Poria* as the fruiting stage of the fungus causing sterile conks on birch. Mycologia **30**: 553–560. 1938.

[3] Campbell, W. A. & Ross W. Davidson. *Poria Andersonii* and *Polyporus glomeratus*, two distinct heart-rotting fungi. Mycologia **31**: 161–168. 1939.

diagnosis. Fertile fruiting on down logs was also noticed. Lorenz and Christensen [4] reported *P. glomeratus* cankers to be common on maples in the Lake States but such cankers have not been reported from New England.

STERILE CONKS AND CANKERS ON BEECH

A number of beech trees bearing sterile conks of *P. glomeratus* (FIG. 1, *A, B*) were cut and dissected. The fungus appeared to infect the trunk chiefly through dead branch stubs, although its association in several cases with trunk wounds could be demonstrated. Infections were particularly common in the upper trunk and the sterile conks were usually seen protruding from knot holes just below the live crown. The decay seemed to progress readily in the heartwood and infections originating in the upper trunk spread down through the heartwood until the entire center of the tree was badly decayed leaving only a narrow ring of sapwood.

Sterile conks frequently formed at old unhealed branch stub openings. These sterile conks, which were obtuse-elongated or flattened, dark brown to black and roughened on the surface from weathering or with rings denoting seasonal activity, rarely protruded more than 3 inches and appeared at first glance to be dead branch stubs (FIG. 1, *B*). In time a decided canker formed on the trunk about the branch stub bearing the sterile conk, and with the appearance and extension of the canker the development of the sterile conk itself seemed to be checked (FIG. 1, *C*). Instead of a marked increase in the size of the sterile conk, sterile fungus material was deposited in the face of the canker so that an ax cut through a canker showed a thick, yellow-brown fungus mass in and beneath the undisturbed bark.

Sterile conks with which no branch stubs were associated were also common, especially on trees badly decayed by the fungus. As the heartwood became decayed the fungus had a tendency to work out through the sapwood often following healed-over branch traces (FIG. 1, *D*). The reaction of the tree in many cases to such outward extension of the decay through the sapwood was to form

[4] Lorenz, Rolland C. & Clyde M. Christensen. A survey of forest tree diseases and their relation to stand improvement in the Lake and Central States. U. S. Dep. Agr. Bureau Pl. Ind. Mimeograph p. 21. 1937.

ridges or fluted areas on the trunk (FIG. 1, *E*). In time the decay sometimes broke through these ridges and a sterile conk formed on the trunk. Later a canker developed around the conk. The development of the sterile conk and canker depended to some extent

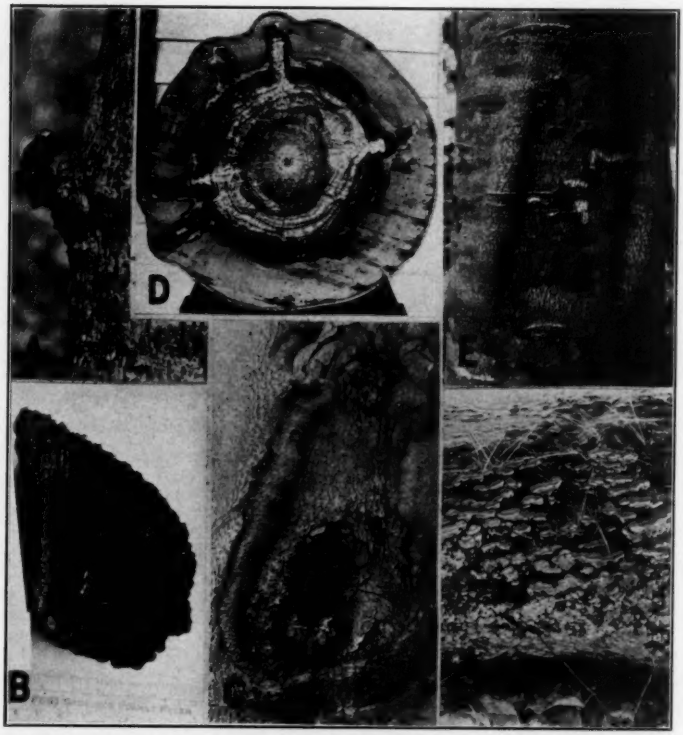

FIG. 1. *Polyporus glomeratus* on beech. *A*, sterile conk on a 5-inch suppressed tree; *B*, sterile conk approximately 3 by 4 inches; *C*, canker showing sterile conk; *D*, cross section of a 15-inch tree decayed by *P. glomeratus* (notice streaks of decay extending into the sapwood); *E*, ridges or fluted areas on trunk; *F*, sporophores of *P. glomeratus* on down log.

on the vigor of the tree. Vigorous, fast-growing trees resisted canker formation and tended to produce more pronounced sterile conks, but slow-growing, non-vigorous trees cankered readily and formed inconspicuous sterile conks.

In most cases the bark did not slough off the surface of the canker but it became much cracked and checked, and the hard yellowish fungus material was deposited in the cracks and beneath the bark itself. These cankers were often very large, especially on old trees, and elongated cankers as much as 2 feet long and somewhat less narrow were not uncommon.

Evidently *P. glomeratus* fruits rarely on living trees. Sporophore formation takes place on the underside of down logs usually several years after the trunk blows over. It occasionally fruits on the side of the upright stump or stub but such fruiting is limited. On the down log the fungus fruits in abundance often forming sporophore masses many feet long on the entire lower side of the trunk (FIG. 1, *F*). The yellowish-green spores are produced in great quantities and often cover the ground and nearby objects with a bright yellowish-green powder.

Sterile conks of *P. glomeratus* are common on the overmature beech in the Green Mountain National Forest, Vermont, and were also found in the White Mountain National Forest, New Hampshire. One sterile conk was collected in Pennsylvania and one in Maine.

STERILE CONKS AND CANKERS ON RED MAPLE

Polyporus glomeratus was associated with well-defined cankers on red maple particularly in connection with old branch stubs (FIG. 2, *A*). Such cankers usually had a definite hypertrophied margin and a depressed center. The depressed center of the canker was filled with a hard crust-like deposit of sterile fungus material, which was often not greatly different in appearance from the maple bark itself. In many cases the canker face, especially if it originated at a point other than a branch stub, was covered by the apparently undisturbed bark which on examination proved to be impregnated with fungus material. Elongated cankers with hypertrophied margins were not uncommon (FIG. 2, *B*). Cross sections of the stems showed marked distortion and swelling and in the field the disease could be readily recognized by the peculiar swollen, often protruding, branch stubs and cankers. Multiple cankers on old red maples often caused large distorted areas on the stem (FIG. 2, *C*).

Definite protruding sterile conks such as were common on beech were rare on red maple. Occasionally, however, a flattened, solid mass of fungus material formed, especially in connection with large cankers. *P. glomeratus* cankers could be readily diagnosed on red maple by making an ax or knife cut into the center of the canker and examining the hard, dark-brown fungus material which was

FIG. 2. Cankers of *Polyporus glomeratus* on red maple. *A*, canker around branch stub; *B*, elongated canker; *C*, multiple cankers on large red maple causing distortion of the trunk.

deposited in and beneath the bark. The rot back of the canker was usually very soft, often with tan-colored mycelial mats filling the rotted areas.

Sporophore formation is similar to that in beech. Fruiting takes place on down logs which have been in contact with the ground for several years. The sporophores are short-lived, especially so in wet weather, and quickly become dark, sodden and insect riddled.

P. glomeratus is evidently an important decayer of red maple and on one area of the Gale River Experimental Forest, New Hampshire, fully one-quarter of the trees were cankered or broken because of the rot. The fungus was also common on the Green Mountain National Forest and was noted to a lesser extent on the Tunxis State Forest, Connecticut and in Pennsylvania. J. R. Hansbrough and T. J. Grant have collected *P. glomeratus* on sugar maple (*Acer Saccharum* Marshall) in Maine.

CIVILIAN CONSERVATION CORPS AND
DIVISION OF FOREST PATHOLOGY,
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ASCUS DEHISCENCE IN LECANIDION ATRATUM AND ITS SIGNIFICANCE

ELLYS T. BUTLER

(WITH 2 FIGURES)

INTRODUCTION

Some years ago a taxonomic study of the Patellariaceae was undertaken with the expectation of including comparative culture work to determine the life histories and relationships of these almost totally unknown forms. The Patellariaceae comprise a family of the inoperculate Discomycetes, placed by most authors in the order Pezizales, in spite of the fact that it is admitted certain species are lichenous and many are "lichen parasites" (**13**). *Lecanidion atratum* (Hedw.) Endl. (*Patellaria atrata* Fries) is the type species of the genus *Patellaria* Fries, for which the family was named (FIG. 1), and is of special interest for its unique method of spore discharge.

The significance of ascus dehiscence in the classification of the Discomycetes has long been an interesting question. Three types of dehiscence are reported for this group; the operculate type, characterized by a circular rupture (ascostome) opening by a lid (operculum), which usually remains attached at one side after spore discharge; the inoperculate type, in which the spores escape at the apex of the ascus through an ascostome which has an elevated or ragged margin, but no definite operculum; and the bilabiate type, in which the opening is a transverse slit at the apex of the ascus (**31**).

In 1879 Boudier (**5**) proposed the division of the Discomycetes, on the basis of dehiscence, into two sections—Operculae and Inoperculae, placing those forms having bilabiate dehiscence with the Operculae. His work was overlooked or ignored by some subsequent writers of texts, and those treating the fungi as a whole, who generally followed the old well known systems of classification, but was adopted by all later students of the Disco-

mycetes, who presumably would be better fitted to evaluate his work. Massee (**22**) thought Boudier's system was impractical, believing the operculum could be observed only in fresh material, but he was mistaken, for these characters may be determined easily in most cases from herbarium material. Boudier (**6**) himself, after further study and consideration of other characters, was convinced that this method results in the most practical and natural classification of the Discomycetes. Lagarde (**21**) thought Boudier's system marked important progress in the recognition of natural affinities in this group. His independent studies in comparative anatomy confirmed Boudier's classification and added new arguments in favor of it. Ramsbottom (**30**) expressed surprise that Boudier's system had not been more generally adopted, and said that these two divisions seemed to have the same importance as the Monocotyledons and Dicotyledons in the Phanerogams. Gäumann and Dodge (**14**), Gwynne-Vaughn and Barnes (**16**), and Bessey (**4**) are among the recent authors of texts who have followed Boudier; and Corner (**10**), Nannfeldt, and Seaver are outstanding authorities on the Discomycetes who uphold Boudier. Seaver (**31**, p. 17) maintains that this offers a morphologically sound basis for a natural division of the group. Nannfeldt (**25**) considers the Discomycetes to be the most primitive forms of his division Ascohymeniales, and divides them into four orders, placing all the operculates in the Pezizales. The remaining three orders contain the inoperculates and most of the discolichens.

REVIEW OF THE LITERATURE

Early in the study of the Patellariaceae the writer realized that the thick walled asci of *Lecanidion atratum* were not typical of the inoperculate Discomycetes. Even more interesting was the fact that an ascostome was never observed. Empty asci were frequently noted where the entire upper third of the ascus had broken off (FIG. 2, *H–J*). The question arose as to whether this breaking off of the upper portion of the ascus, as a thimble-like cap, was the natural method of dehiscence for this species. A search through the literature brought together several different opinions

on this question. Hedwig (**17**) believed that with the accumulation of water the spores were discharged through the elasticity of the asci. He was uncertain of their subsequent history after they became dry, but thought they were probably dispersed by the wind. His illustration of a vertical section of an apothecium

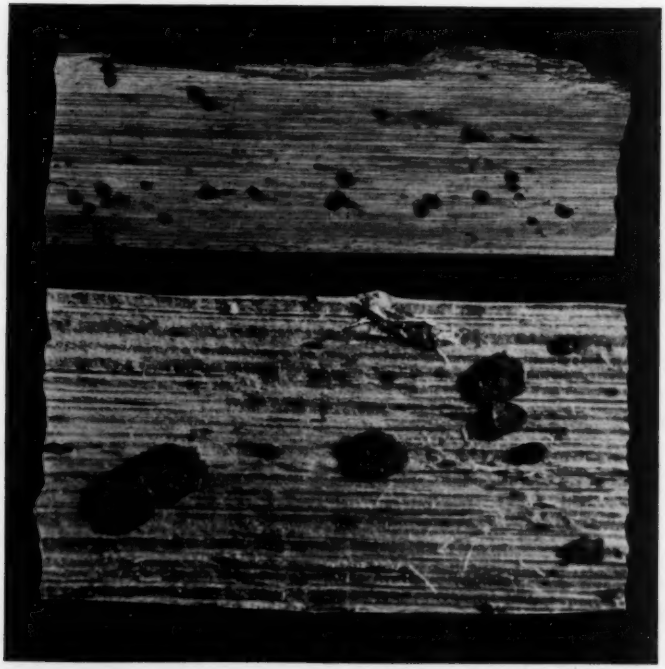

FIG. 1. Upper figure, scattered apothecia of *Lecanidion atratum* on *Agave* stem, × 2; lower figure, apothecia of the same, enlarged 12 ×.

shows the heavy epithecium still intact, and numerous spores floating above it.

Nees (**26**) says that the spores are ejected from the asci when a dry specimen is placed under water. He thought they must be ejected through the lower end of the ascus where it is attached, as he never saw an opening in the upper part. His illustration also shows numerous septate spores above the apothecium.

Crouan and Crouan [1] (**11**) said that the clavate ascus, when it is about to shed its spores, lengthens, and contracts above forming a beak at its tip. The spores go out through a narrow opening one after the other, and as each spore passes out there is a sort of recoil, which throws it; those which go out last produce so forceful a recoil that the ascus springs back like a cannon after it hurls its projectile. They thought the ring-like constriction near the center of an empty ascus was due to a redoubling of the internal membrane.

Boudier (**5**, p. 45) criticized these observations of the Crouans saying ". . . they imperfectly saw another mode of dehiscence in *Lecanidium atrum* (=*Patellaria atrata* Fr.), but they described it badly, for the sporidia, in all the Pezizae are discharged at the same time." He later published illustrations that must have been his own idea of spore discharge in this species (**7**). His figure *i* shows the apex of an empty ascus with an immarginate foramen. Figure *j* he says represents the upper portion of asci after their dehiscence, showing the debris of the membranous sac that envelops the spores and that is often found projecting from and remaining attached to the foramen in the form of a collarette. The writer, as stated before, has never observed an ascostome in *Lecanidion atratum* as illustrated in Boudier's figure *i*. The projecting collarette, shown in his figure *j*, is more understandable although it has never been seen in that form.

OBSERVATIONS

A recent collection [2] of this species on weathered *Agave* stems, has made possible the study of ascus dehiscence in living material. These specimens had been air dried and were brought into the laboratory about six weeks after the date of collection. Small

[1] " La thèque est claviforme, on aperçoit quand elle va disséminer ses spores, qu'elle s'étire ou s'allonge en s'atténuant en bec à son sommet, les spores sortent par l'ouverture étroite les unes après les autres et à chaque spore qui sort il y a une espèce de détente qui la lance, celle qui sort la dernière produit une si forte détente que la thèque recule en arrière comme le ferait un canon après avoir lancé son projectile. La thèque étant vide on aperçoit vers son milieu un étranglement ceint par un cercle ou anneau; nous pensons que ce singulier phénomène est dû à un dédoublement de la membrane interne."

[2] Seaver, F. J., Waterston, J. M. and Russell, T. A. Bermuda fungi no. **85**.

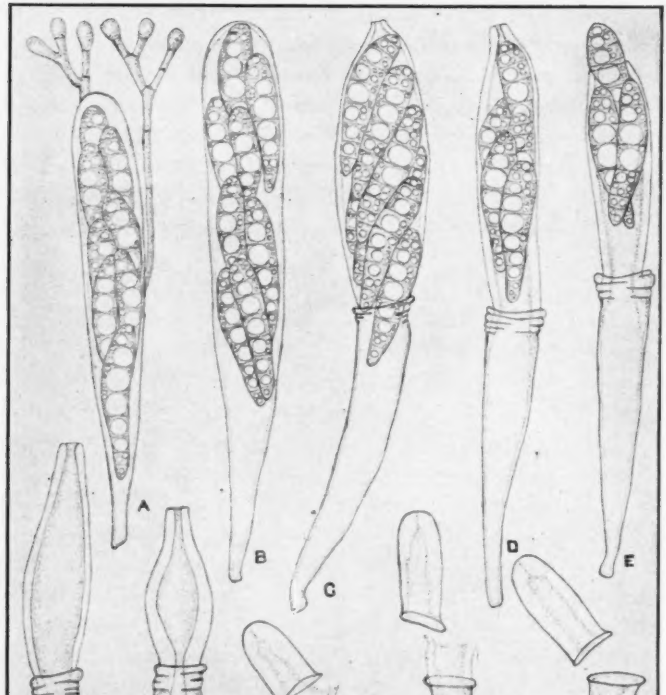

FIG. 2*A*, paraphyses and ascus of *Lecanidion atratum; B*, elongated ascus immediately before dehiscence; *C*, ectoascus ruptured at apex and rolled back, endoascus elongating; *D*, spores discharging from apex of endoascus; *E*, spore squeezing through opening at apex of endoascus; *F*, empty ascus immediately after spore discharge; *G*, empty ascus showing typical swelling of endoascus; *H–J*, empty asci with thimble-like caps formed when ectoascus breaks below the apex.

blocks of wood bearing mature apothecia were cut out and placed on moistened filter paper in inverted petri dishes containing corn meal agar. The plates were kept at room temperature (about 20° C.) and 12 hours later the surface of the agar, 5 mm. above the apothecia, was found sprinkled with ascospores. Additional spores were discharged from the same apothecia on the four following days. Numerous apothecia were set up in this manner and examined for method of ascus dehiscence during the days of spore discharge. A free hand section of an apothecium was cut and placed on a slide in a drop of water, covered with a cover slip applied with as little pressure as possible, and studied under the microscope. Some asci were injured in sectioning, broken from the hypothecium and floated free in the water, but where the hymenium had been least disturbed and the asci were still attached, spore discharge occurred in the following manner, without the addition of any poisonous stimulant such as Buller used (**8**). The mature turgid asci were 155–179 μ long, extending to the tips of the paraphyses, with the spores crowded in the upper two-thirds of the asci, the upper one pressed against the apical wall which was not thickened (FIG. *2B*). (Asci measured in this material before it was placed in a moist chamber averaged 115 μ in length.) The outer ascus wall ruptured at or near the apex and rolled back (FIG. *2C*), while at the same time an inner membrane surrounding the spores pushed up above the epithecium. (The term "endoascus" will be used to designate this inner membrane, and the term ectoascus might be applied to the outer wall.) This happened very quickly, the spores being carried up above the ring formed by the outer wall, although two or three spores sometimes remained below this ring. After a few seconds, during which the endoascus continued to lengthen, until it extended above the epithecium nearly one-third the length of the ascus, the spores were shot out successively with considerable force from the apex of the endoascus. The first four spores were shot out in rapid succession, the last ones more slowly, so that the process could be followed easily (FIG. *2D*). A spore pushed forward to the apex and, stretching the contracted pore, slowly squeezed through the opening to the point of the maximum width of the spore and then was shot out quickly and forcefully (FIG. *2E*). Thus the shape of the spore seems to play an important part in its discharge.

Seaver (**31**, p. 20) described this process of stretching and contracting in the operculates, but he was unable to follow the discharge closely as there was no pause between spore ejections and the motion was too rapid.

In *Lecanidion atratum* the endoascus recoiled slightly and another spore took its place at the apex, the entire endoascus then lengthened gradually while this spore was slowly pushing through the opening and when nearly the original length was reached the spore was discharged. This continued, the process gradually slowing down, until all the spores had been discharged, although frequently one, more rarely two spores remained within the ascus. The dehiscence of more than 50 asci in water has been watched, and in every case the process was exactly the same as that described above, the only variation being in the time intervals. Usually the spores were discharged immediately after rupture of the outer wall and extention of the endoascus. Sometimes there was a pause after the rupture of the ectoascus and extension of the endoascus, up to three minutes in duration, before the first spore was discharged. Three spores were discharged per second, or there was an interval of two to five seconds between each spore, occasionally an even longer interval in the case of the last spores in the ascus. Immediately following the discharge of the last spore in every case the endoascus shrinks in length and width to one-half or one-third its maximum size, thus withdrawing nearly to the level of the epithecium. It then swells leaving a very narrow opening (FIG. *2G*). This may be the collarette of Boudier, but as figure *2G* shows, it is not the same in appearance. The Crouans, believing the entire ascus elongated, missed the fact that the beak-like tip was the apex of an inner membrane. The ring-like constriction in the center of the ascus that they mention was probably the broken outer wall, as shown in my figure *2F*. Isolated asci also frequently discharge their spores in this manner, although in three unique cases the spores were shot out successively and with force from the torn lower end of the ascus.

DISCUSSION

As far as can be determined, this type of spore discharge from an endoascus, characteristic of certain species in the Sphaeriales, Dothideales, and Myriangiales, has never been reported in the

Discomycetes. In fact, deBary (**2**) stated it was unlikely that successive ejection would occur in the open hymenia of the Discomycetes. Currey (**12**) reported and illustrated this type of dehiscence in *Sphaeria herbarum*. Pringsheim (**21**) was the first to give a detailed account, well illustrated, for *Sphaeria Scirpi* (= *Pleospora scirpicola* (DC.) Karst.) and it is now frequently referred to as the "*Sphaeria Scirpi* method of dehiscence." Sollman (**34**) illustrated the same type in three other species of *Sphaeria, S. inguinans, S. ellipsocarpa,* and *S. lanata;* and Woronin (**3**) in *S. Lemaneae.* It has been reported in the following Sphaeriales: in *Cucurbitaria Laburni* by von Tubeuf (**39**); in *Ascospora Beijerinckii* by Vuillemin (**40**); in *Leptosphaeria acuta* by Hodgetts (**18**); in *Physalospora malorum* by Shear and Stevens (**33**); in *Ascospora ruborum; Mycosphaerella rubina,* and *Venturia inaequalis* by Zeller (**41**); in *Metasphaeria Asparagi* by Tehon and Stout (**38**); in *Melanomma* and *Sporormia intermedia* by Ingold (**20**) who called it "jack-in-the-box" dehiscence; in *Sporormia bipartis* by Page (**27**), and in certain species of *Pleospora* and in *Pyrenophora* by Atanasoff (**1**), differing in this case in that the inner wall ruptures not at the apex but just above the ring formed by the contracted outer wall.

Hoggan (**19**) observed this method of dehiscence in *Plowrightia ribesia* and suggested that it indicates a close relationship between the Dothideales and Sphaeriales.

Various interpretations have been given to the ascus structure in the Myriangiales. Miles (**23**) considers the ascus in *Myriangium tuberculans* thin walled, but surrounded by the inner sheath of the locule which separates from the stromatic tissue and remains closely attached to the ascus until it ruptures and collapses about the base of the expanding ascus. Stevens and Weedon (**36**) are uncertain whether *Kusanoopsis guianensis* has the rare condition of an ascus with double walls or merely that the spores protrude, surrounded by a quantity of epiplasm. Tai (**37**) reports a double wall in the dehiscence of *Myriangium Bambusae,* saying that this character, with others, indicates relationship with the Sphaeriales. It has also been reported in *Myriangium Duriaei* by Millardet (**24**) and by Petch (**28**), and in *Myrianginella Tapirae* by Stevens and Weedon (**36**, p. 199, f. 9).

Ziegenspeck (**42**) found this type of dehiscence in only one of the lichens, in *Nephroma tomentosum*, a species with open apothecia, classified in the Cyclocarpineae, family Peltigeraceae (**35**).

In a number of cases it was reported that the outer wall broke below the apex and the thimble-like cap thus formed was pushed up by the expanding inner membrane. This was illustrated for *Sphaeria lanata* (**34**), *Sphaeria herbarum* (**12**), *Leptosphaeria acuta* (**18**), *Sporormia leporina* (**9**), and used by Griffiths (**15**) as a basis of classification of *Sporormia, Sporormiella,* and *Delitschia.* Hodgetts (**18**) and Cain (**9**, p. 12) thought this might be an unnatural mode of dehiscence in some cases, due to artificial pressure. This would seem to be the case in *Lecanidion atratum* where the thimble-like caps were commonly found in crushed mounts, but were never observed in actual ascus dehiscence under more nearly normal conditions. It may be that the outer wall breaks in different places, as has been recorded for some of the Sordariaceae (**15**, p. 34). When it ruptures below the apex the cap might be carried up by the elongating endoascus, or quickly pushed off.

Nannfeldt has included the above mentioned forms, with the exception of *Nephroma,* in his new group Ascoloculares which he says is characterized by having the asci borne within stromatic bodies with no true perithecial wall and no true paraphyses, and by the *Sphaeria Scirpi* type of dehiscence. In the group Ascohymeniales are genera with thin walled asci, thickened only at the tips, with the exception of the disco-lichens, and certain closely related Discomycetes, namely *Patellaria,* where the ascocarps have a longer life span and the asci are thick walled. Since he believed that they do not have an endoascus type of dehiscence, being provided in every case with an ejaculation mechanism at the apex, he included them in the Ascohymeniales. Nannfeldt placed *Lecanidion* with most of the discolichens in the order Lecanorales, of the Ascohymeniales, distinguished by the usual presence of symbiotic algae, the long lived cartilaginous apothecia, the thick walled asci which stain blue with iodine and the heavy epithecium formed by the paraphyses. He (**25**, p. 62) pointed out the resemblance of these asci to those of the Ascoloculares and emphasized that they may be distinguished by their positive iodine reaction, and by the pore type of dehiscence. Obviously Nannfeldt had not seen spore

discharge in *Lecanidion,* and probably relied on Boudier's descriptions and illustrations.

Ascus dehiscence is considered a most reliable criterion upon which to base large group relations in the Ascomycetes, as has already been pointed out. Thus the discovery in the Discomycetes of this endoascus type of dehiscence, which was thought to be restricted to certain Pyrenomycetes, or the Ascoloculares according to Nannfeldt, leads to several interesting possibilities. It seems to be an indication of the relationship of *Lecanidion atratum* to those Pyrenomycetes, or the same type of dehiscence may have evolved in several widely separated groups. The Patellariaceae have been considered a connecting link between the Pezizales and Phacidiales and Hysteriales, which in turn lead to the Sphaeriales. One might expect, therefore, a similar method of spore discharge. As Shear (**32**) has suggested, we may have placed too much emphasis on the importance of the form of fructification in arbitrarily separating Discomycetes from Pyrenomycetes.

As our knowledge of the morphology and life histories of the inoperculate Discomycetes and disco-lichens increases, it will be important for students of these groups to note the mechanism of spore discharge. The endoascus type of dehiscence may be another much needed character to help clarify the relationships of some of these perplexing forms on the border line between the Pyrenomycetes and Discomycetes and lichens, especially in the Patellariaceae, Phacidiaceae and Tryblidiaceae. When this knowledge is correlated with that obtained as the result of other studies, it may be found that our large group of inoperculate Discomycetes naturally falls into two groups, those with an ascostome and those without an ascostome, but with a functional internal membrane.

SUMMARY

Lecanidion atratum, which has been placed with the inoperculate Discomycetes, has a method of spore discharge unique for that group. The outer ascus wall breaks at, or near the apex and rolls back; an inner membrane, here termed the endoascus, pushes up above the epithecium nearly one-third the length of the ascus; the spores are then shot out successively and forcefully from the apex of the projecting endoascus.

This endoascus type of dehiscence is characteristic of certain Pyrenomycetes, but has not before been reported in any of the Discomycetes. On the basis of this character, which is considered a reliable indicator of relationships, the Patellariaceae seem to show a closer relationship with certain Pyrenomycetes than with the other inoperculate Discomycetes. It may also prove to be an additional criterion of value in determining the natural classification of the inoperculate Discomycetes and disco-lichens.

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A NEW SCLERODERMA FROM BERMUDA

W. C. Coker

(with 1 figure)

Scleroderma bermudense sp. nov.

Fructificationes subglobosae, 1.8–2.8 cm. crassae, omnino subterraneae ad maturitatem, undique sparsim delicatis brunneis araneosis fibrillis investitae, ex quibus flocculosae fibrae in solum extendunt, apice in 5 vel 6 lacinias stellatas dehiscentes; peridio siccato 1–1.5 mm. crasso et distincte scissili; peridio humido circa 2–2.5 mm. crasso, praeter fibrillas liberas, ex strato tenuissimo laxo externo circa 0.12–0.18 mm. crasso et strato interno multo fusciore compacto composito.

Sporis brunneis, globosis, echinulato-verruculosis et granulosis, 6–7.5(8) μ, paucis per partes reticulatis.

Fruit body subglobose, 1.8–2.8 cm. thick, entirely subterranean until dehiscence, the entire body thinly covered with delicate brown arachnoid fibers which hold fine particles of sandy soil and from which flocculent strands extend into the soil. Dehiscence as in *S. Geaster* but rather more regular than in that species, the lobes usually five or six. Peridium when dry about 1–1.5 mm. thick and distinctly scissile, when soaked about 2–2.5 mm., consisting, in addition to the free fibers, of a very thin, loosely woven paler outer coat about 0.12–0.18 mm. thick and a much darker, dense portion which in thin section shows varying layers of lighter and darker flesh, the innermost layer black.

Spore mass earthy brown (faintly olive), very friable and easily completely shaken out of the peridium; spores brown, globose, minutely spiny-warted and scurfy, 6–7.5(8) μ, a few with a partial reticulum; some fibrous fragments mixed with the spores.

Bermuda Islands. In sand, Grape Bay, Nov. 29, 1938, No. *15A*. Buried in sand when young, Elbow Beach, Dec. 4, No. *119;* Dec. 11, No. *183*. All collections by F. J. Seaver and J. M. Waterston.

This *Scleroderma* is nearest *S. Geaster,* from which it easily differs in its delicate attachment to the soil over its entire surface and the absence of any more specialized basal attachment by compacted strands and plates, by its much smaller size, thinner and less tough peridium, and by the ease with which the gleba is

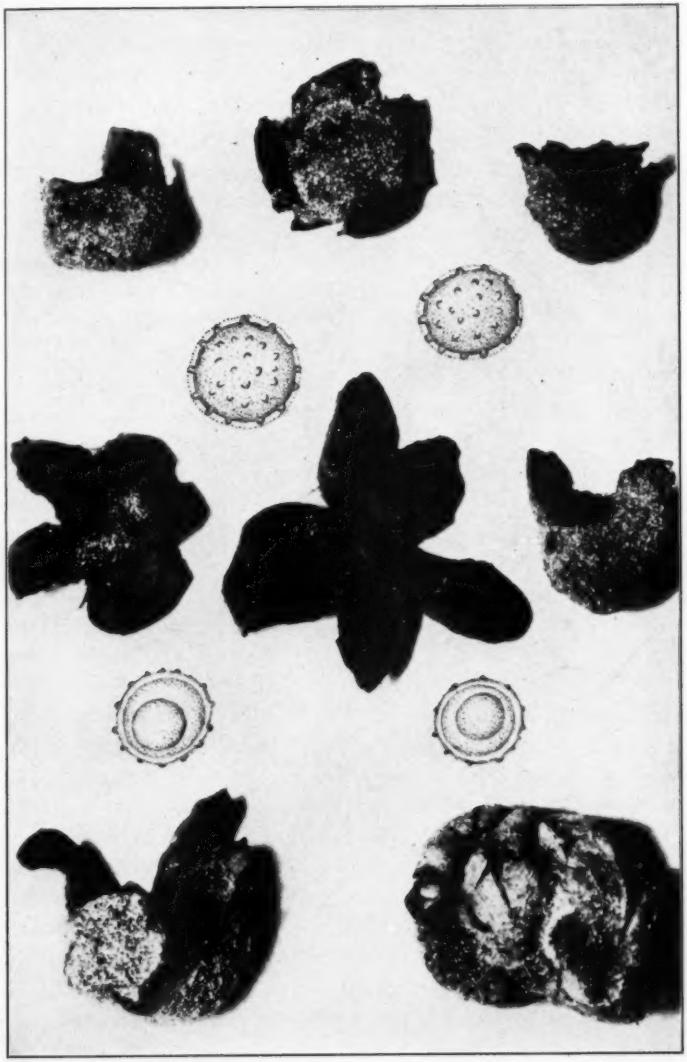

FIG. 1. *Scleroderma bermudense.*

freed from the peridium and can be shaken out as a whole. In most cases the outer coat is dotted all over with small white grains of sand which can be rather easily rubbed off. The spore drawings and the Latin diagnosis are by Miss Alma Holland and the photograph by Miss Laurie Stewart, both of this department.

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EXPLANATION OF FIGURE

FIG. 1. *Scleroderma bermudense.* Photographs of fruit bodies in various stages of maturity. In center, remains of old periderm after spores have been dispersed. All photographs natural size. Drawings of four spores in various stages of development × 1000.

NOTES AND BRIEF ARTICLES

The Problem of Gamete Production in Blastocladia

I have read with interest and concern the claim made by Dr. Ernst A. Bessey that he has observed isoplanogametes in *Blastocladia Pringsheimii;* and while I do not deny this claim, I wish that it were better substantiated: that he could have observed more than one case of fusion, and that he could have known the source of these "gametes."

Blastocladia Pringsheimii Reinsch has been under continuous observation in the grounds and laboratory of Royal Holloway College, University of London, for the past six years. During that time thousands of plants have been examined, and all plants that have ultimately borne resistant sporangia, have previously borne thin-walled sporangia. No plants have been found to bear resistant sporangia only.

From summer 1933 to summer 1935 plants were examined every month (Lloyd **1938**), and emission of swarmers from the thin-walled sporangia frequently watched, and never was fusion observed, but instead the swarmers were seen to germinate directly. Miss Lloyd says: "Fields of motile zoospores have been watched to see if zoospores from different sporangia or from sporangia which are borne on different plants show any tendency to fuse. The zoospores vary somewhat in size and some zoospores are less active than others, but from their behaviour there has been no suggestion of a larger female and a smaller male gamete. The flagella of two zoospores have frequently become intertwined; they have, however, always separated later by their own tugging or by the intervention of a third zoospore. Two zoospores have often been seen to come to rest side by side and undergo amoeboid movements, and then one or both have swum away. It is possible that the right combination of gametes (if they are such) has not been obtained, but as many fields of mixed spores have been watched and as germination without fusion has been seen in no less than thirty-two of these it seems unlikely that the zoospores are gametes."

On many occasions since September 1937 quantities of thick-walled resistant sporangia have been germinated (Blackwell **1937**) and the swarmers liberated have never been seen to fuse, though many have been watched closely. Instead these swarmers have germinated directly as in the case of swarmers from thin-walled sporangia.

Various thin-skinned berries (of spp. of *Vitis, Lycopersicum, Solanum,* etc.) have been inoculated with swarmers from resistant sporangia and within two days pustules of fully formed plants of *Blastocladia Pringsheimii* have appeared on the skin. These have borne thin-walled sporangia whose swarmers have been carefully watched and never been seen to fuse, but instead have germinated directly.

During the spring of 1939 Dr. Ralph Emerson applied his delicate and precise technique for isolating swarmers to the material in this laboratory. He isolated zoospores from resistant sporangia and succeeded in germinating them singly *in pure culture* on corn meal agar (Difco). The plants which developed were observed very closely; they bore thin-walled sporangia and liberated swarmers. These swarmers showed no signs of fusion and germinated directly to give new plants like their immediate parent.

While it is admitted that *Blastocladia Pringsheimii* may like *Allomyces Kniepii* (Sörgel **1937**) have more than one type of life history and that Dr. Bessey may have a different strain from ours; until the source of the fusing "gametes" is known and more than one instance of fusion observed, the case for isoplanogametes, though possible, can scarcely be said to be proved.—ELIZABETH BLACKWELL.

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